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ZOOGEOGRAPHY OF THE ACRIDOIDEA (INSECTA: ORTHOPTERA) IN THE CANARY ISLANDS

by

Christina Marie Holzapfel

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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Doctoral Committee:

Associate Professor Irving J. Cantrall, Chairman
Professor Theodore H. Hubbell
Professor Robert R. Miller
Professor Warren H. Wagner, Jr.

ABSTRACT

ZOOGEOGRAPHY OF THE ACRIDOIDEA (INSECTA: ORTHOPTERA) IN THE CANARY ISLANDS

by

Christina Marie Holzapfel

Chairman: Irving J. Cantrall

Forty-six species of Acridoidea (Orthoptera) are found in the Canary Islands. They represent a diverse fauna of ten subfamilies and twenty-two genera.

A large portion (43%) of the grasshopper fauna is endemic. Nine of the species belong to wingless taxa and offer special problems in dispersal and adaptation. The explanation of the geographic origin of these and non-endemic taxa is complex due to faunal shifts since the Tertiary and paucity of knowledge of the fossil record in Africa and Eurasia. However, most of the endemic members have close modern affinities with taxa in Africa. Six non-endemic species occur only in Africa and the Canary Islands, and the remaining twenty species are known from combinations of Africa, Europe and southwestern Asia.

The Acridoid fauna is most diverse on the two largest central islands in the archipelago, Gran Canaria and Tenerife. The continental eastern islands and the small western islands house impoverished faunas.

In order to gain an insight into the ecological preferences of the Acridoid fauna, species were classified according to their occurrence in the four major vegetation belts on the Islands. Most species occupy areas below the subalpine zone (1500 meters) and above the beach zone. When taxa are distributed in more than one zone, the zones are always adjacent; in no case is a species adapted to non-contiguous zones.

Several lines of evidence suggest that much of the Acridoid fauna of the Canary Islands is rather recent in origin. Although several endemic species have been rarely collected on adjacent islands, only five are established on more than a single island. These observations suggest that the endemic fauna is in the expansion phase. Sympatry is the exception rather than the rule. Twenty-two of the 46 species are known from only a single island. Of these, nine are winged non-endemic forms, most of which I believe share gene pools with mainland counterparts. Among non-endemic species, little morphological differentiation has occurred. Only in Dericorys has differentiation advanced to the subspecific level.

Although a number of wingless species occur on the Canary Islands, aptery in the Acridoids does not represent an adaptation to insular conditions. The closest relatives of the wingless species of the Canaries occur in continental Africa, and are themselves wingless or micropterous. In fact, there is a higher occurrence of reduced-wing taxa in the Acridoidea of Africa than on the Canary Islands.

Methods of multiple regression analysis were used to study the relationship between numbers of species of Acridoidea and vascular plants to topographic features of the Islands. These features included surface area, distance from the mainland, maximum elevation, island complexity and nearest neighbor. It was found that, for the Acridoidea, number of species on an island is affected about 48% by surface area available for habitation, 38% by elevation and less than 1% by distance from the mainland. Number of species of vascular plants may best be predicted by knowledge of the maximum elevation (about 80%), and to a lesser extent by surface area (35%). Again distance from the mainland is rather unimportant in determining total numbers of species present. An independent method of testing the importance of area and elevation in this system was devised; results of these tests confirm the conclusions based on regression analysis.

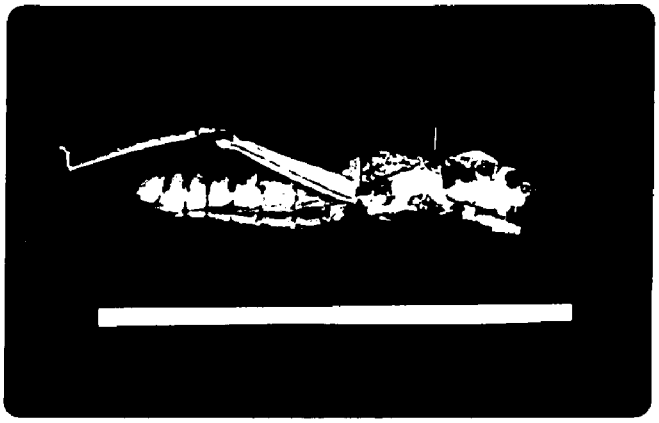
Frontispiece. Specimens of Canary Island Acridoidea illustrating variation in habitus.

A. Acrostira bellamyi Uvarov (Hermigua, Gomera)

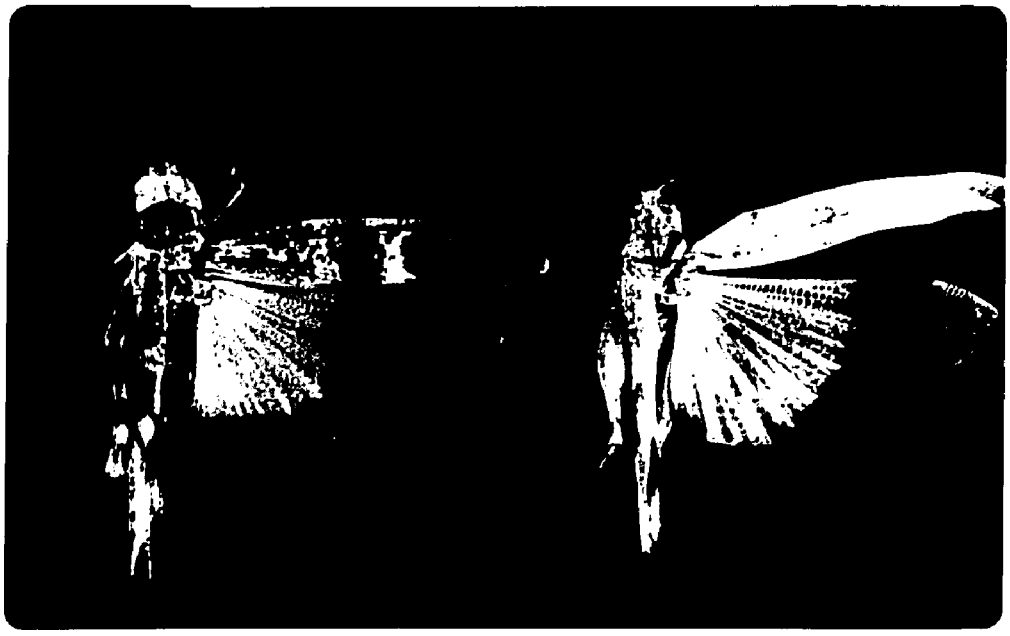
B. Scintharista notabilis notabilis Walker (Barranco Ville, Gomera)

C. Oedipoda caerulescens Linnaeus (Vilaflor, Tenerife)

D. Truxalis nasuta Linnaeus (Las Palmas, Gran Canaria)

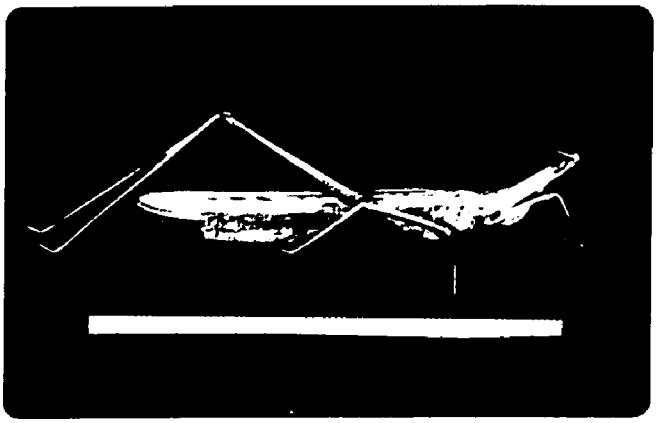


A



B

C



D

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First and foremost, I wish to thank Dr. Irving J. Cantrall for his continued assistance in my studies of Acridoidea, for his learned criticisms of many of my manuscripts, and for his thoughtful manner in directing my independent study.

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Naturhistoriska Riksmuseet, Stockholm, Sweden

Rijksmuseum Van Natuurlijke Historie, Leiden, Netherlands

National Museum in Prague, USSR

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Zoologisches Staatinstitut & Zoologisches Museum, Hamburg, Germany

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ABBREVIATIONS USED IN VEGETATION LISTS

Life form symbols (after Raunkiaer, 1934)

M = macrophanerophyte (tree, over 2 meters)

N = nanophanerophyte (shrub, 0.3 - 2 meters)

Ch = chamaephyte (renewal buds between soil level and 0.3 meters)

H = hemicryptophyte (renewal buds at soil level)

G = geophyte (renewal buds below soil level)

T2 = biennial

Th = therophyte (annual)

SS = stem succulent (permanent stem succulent)

Braun-Blanquet coverage classes

\+ = less than 1%

1 = 1-5%

2 = 6-25%

3 = 26-50%

4 = 51-75%

5 = 76-100%

INTRODUCTION

The past ten years mark the rebirth of interest in the biology of islands, those peculiar isolated regions which hold the key to our understanding of many evolutionary problems. MacArthur and Wilson's equilibrium theory of island biogeography (1963) opened a new avenue for ecological interpretation of island biotas. Sherwin Carlquist's "Island Life: A Natural History of the Islands of the World" (1965), did much to collate the scattered data on island forms into a summary of the history and destinies of many groups. Several expeditions have been made to archipelagos by scientists interested in diverse fields of geology, botany and zoology. An eleven-man team of Europeans led by Dr. Alfons Evers of Krefeld, Germany, collected widely in the Canary Islands during the years 1965-66; "The Galápagos" (1966) is, in part, a result of an expedition to those islands in 1964 organized by the Galápagos International Scientific Project. In spite of these efforts, as Hubbell (1968) well states, what must be stressed is ". . . not how much, but how very little we actually know about the biology of islands..." Even in an area as well studied as Hawaii, investigation of almost any group of plants or animals seems to reveal new species and unknown evolutionary phenomena.

My interests in the theoretical aspects of island endemism and adaptation depended upon a thorough understanding of some plant or animal group from a major island system. The Canary Islands were

selected as an appropriate study area for several reasons. These islands represent a relatively undisturbed area. Man has had a major impact only in deforestation, and even here, native areas may still be found for systematic study. Many investigators have been attracted to this region of the world, in part, by the many natural resort areas on the islands. As a result, almost all groups of vascular plants and animals have been widely collected, and are available for study.

The Acridoidea (Orthoptera) are abundant on the Islands at all times of year and the group is relatively well known on the adjacent mainland areas, Africa and the Iberian Peninsula. Therefore, this group was chosen for study.

The purpose of the first section of this report is to provide a summary of the known information concerning the Acridoidea of the Canary Islands. In the second section, I have used this information to interpret several evolutionary problems of current interest, such as the relationship between aptery and insular habitation, and the correlation between species diversity and topographic features of the islands.

CHAPTER ONE: DISTRIBUTION, ECOLOGY AND SYSTEMATICS OF THE ACRIDOIDEA OF THE CANARY ISLANDS

The Canary archipelago is located in the North Atlantic Ocean about 100 miles northwest of the coast of Rio de Oro at approximately 28^{O} North latitude (Map 1). There are seven major islands and five very small islands in the system. Gran Canaria, Tenerife, Gomera, La Palma and Hierro, the five most western, are strictly oceanic in origin; the eastern islands, Lanzarote and Fuerteventura, are continental and were probably connected to the African mainland as recently as the Pleistocene (Hausen, 1958; 1959). The Canary Islands are volcanic in origin and are thought to have been formed during the Atlas orogeny in the Tertiary (Ceballos and Ortuño, 1951).

The flora and phytogeographic origins of the vascular plants of the Canary Islands are well known, owing to the major works of Lems (1958, 1960), Pitard and Proust (1908), Burchard (1929) and others. Although many insect collections have been made on the islands, and numerous short reports have been published on isolated findings, no one has tried to assemble the available information or to clarify systematic and zoogeographic relationships of the insect fauna of the Canaries.

It is the purpose of Chapter One to compile information in the literature, data collected during my 1965-66 collecting trip on the Islands, and information deduced from morphological studies of

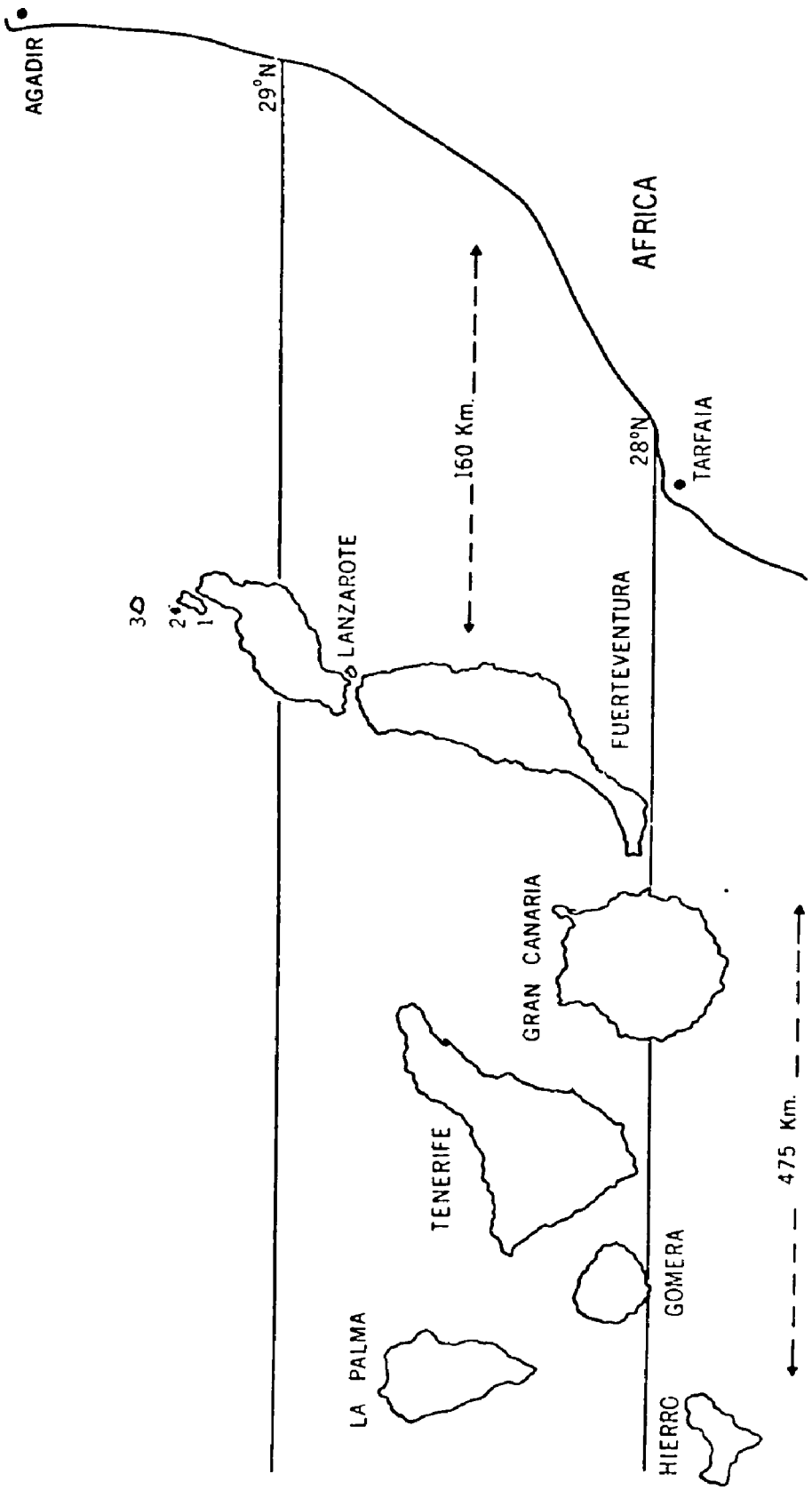
MAP 1. Relative position of the Canary Islands and Africa.

Small outcroppings north of Lanzarote are

1) Graciosa

2) Montaña Clara and

3) Alegranza.


AGADIR
29°N
AFRICA
160 Km.
28°N
TARFAIA
30
2
1
LANZAROTE
FUERTEVENTURA
GRAN CANARIA
TENERIFE
LA PALMA
GOMERA
HIERRO
475 Km.

specimens, into a summary of the known geographic, ecological and systematic status of the Acridoidea of the Canary Islands.

MATERIALS AND METHODS

Before my trip to the Islands in 1965-66, a taxonomic list of the Acridoidea reported from the Canaries was prepared, based mainly on the works of Willemse (1936; 1949; 1950) and Johnston (1956). Although 44 species of Acridoidea had been reported from the Canary Islands, the ecology and specific distribution of the species were largely unknown.

I collected widely on all of the islands, hoping to increase knowledge of this fauna. To supplement my own collections, loans of specimens were received from European museums. With few exceptions, I then had specimens representing all taxa of Acridoidea available for study.

A map illustrating the distribution of each species was prepared. The insular distributions dealt with herein are based on specific collection sites of specimens seen by me or published in the literature. Non-insular distributions of Canarian species or their relatives are those cited in the literature. The most important reference works used in determining non-insular ranges were Johnston's "Annotated Catalogue of African Grasshoppers" (1956), his "Annotated Catalogue of African Grasshoppers Supplement" (1968), Dirsh's "The African Genera of Acridoidea" (1965), and secondary references cited therein.

Whenever appropriate, a list of plant species was prepared for each collection area. Plant coverage[1] was estimated according to the method of Braun-Blanquet (1932).

The course of evolution of the genus Wernerella on the Canary Islands is proposed. This proposal is based on a phenetic analysis of morphological characters after the method of Lems and Holzapfel (1968). Briefly, this method requires equal weighing of characters, and preparation of a table of similarity of species compared two at a time.

Throughout the text, body length refers to a measurement from the fastigium to the tip of the caudal femur.

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[1] Coverage refers to the area of surface covered (or the volume of space occupied) by individuals of a species.

KEY TO THE SPECIES OF ACRIDOIDEA IN THE CANARY ISLANDS

1(8) Fastigial furrow present, lower basal lobe of the hind femur longer than the upper.....2

2(5) Head acutely conical, apical fastigial areolae present, Krauss' organ absent ..... PYRGOMORPHIDAE; PYRGOMORPHINAE. 3

3(4) Wings colorless or pale violet; lateral lobes of the pronotum with lower lobe very deeply concave and with posterior angle prolonged and strongly pointed...Pyrgomorpha cognata Krauss

4(3) Wings red-colored near the base; lateral lobes of the pronotum with lower border barely concave, posterior angle weakly prolonged into a small point..... .....Pyrgomorpha tereticornis (Brullé)

5(2) Head not conical, apical fastigial areolae absent; Krauss' organ present.....PAMPHAGIDAE; PAMPHAGINAE . 6

6(7) Antennae 15-segmented; elytra and wings absent in the female, vestigial in the male..... Acrostira bellamyi (Uvarov)

7(6) Antennae with 11 or 12 segments; elytra and wings vestigial, not reaching the metanotum in the female, in male narrowly lobiform, lateral, exceeding the middle of the first abdominal tergite.....Purpuraria erna Enderlein

8(1) Fastigial furrow absent; lower lobe of the hind femur shorter than or equal in length to the upper lobe..... ACRIDIDAE . 9

9(14) Hind femur with basal lobes of equal length, pronotum with a crest in the prozona..... DERICORYTHINAE. Dericorys .10

10(13) Male body length 19 mm or more as measured from the fastigium to the knee of the hind femur; elytra and wings well surpassing the knee of the hind femur .....
.....Dericorys lobata (Brullé) .11

11(12) Tubercles of the integument strongly black-pigmented; crest of the prozona equal in height to that of the metazona.....
..... Dericorys lobata lobata (Brullé)

12(11) Tubercles of the pronotum without black pigmentation; crest of the prozona higher than that of the metazona.....
.....Dericorys lobata luteipes Uvarov

13(10) Male body length less than 15 mm; elytra and wings terminating at the knee of the hind femur.....
..... Dericorys minuta Chopard . 14

14(9) Hind femur with basal lobe distinctly shorter than the upper; pronotum usually without a crest in the prozona..... 15

15(34) Prozonal process or collar present..... 16

16(31) Mesosternal lobes rounded or obtuse angular, or acute angular, but never rectangular..... 17

17(20) Frons vertical; tip of male cerci pinchers-like, strong, regularly incurved; epiphallus discoidal, without lophi 18

18(19) Wings hyaline to gray; penis valves hidden from above by membranes; tip of male cercus with a broad upper lobe and a weak lower lobe..... Calliptamus plebeius (Walker)

19(18) Wings bright pink; penis valves visible from above, not hidden by membranes; tip of cercus of male with upper and lower lobes of about equal size.....
.....Calliptamus barbarus barbarus (Costa)

20(17) Frons oblique; male cerci variable, but not pinchers-like; epiphallus always with lophi..... 21

21(22) Alate; dorsum of the pronotum deplanate or weakly tectiform; male cercus with compressed, lobiform or subacute, down-curved apex.....
EYPREPOCNEMIDINAE. Eyprepocnemis cinerea (Blanchard)

22(21) Apterous; dorsum of the pronotum of various shapes; male cercus variable, but not with strongly compressed, lobiform or subacute, down-curved apex..CATANTOPINAE. Arminda .23

23(24) Integument tuberculate; pronotum with flattened dorsum, which is somewhat convex in anterior part of the prozona, lateral carinae irregular, callous, divergent; female subgenital plate with five-lobed apex .....
.....Arminda (Chopardminda) canariensis Morales Agacino

24(23) Integument mostly smooth; pronotum subcylindrical, lateral carinae incurved, regular, not callous; female subgenital plate with angular or bilobate apex .... Arminda (Arminda) . 25

25(26) Body length of male more than 15 mm, female greater than 20 mm; dorsal lobes of the aedeagus with out-curved membranous extensions ..... Gran Canaria (Tenerife). Arminda burri Uvarov

26(25) Body length of male less than 15 mm, female less than 20 mm; dorsal lobes of the aedeagus of various shapes, but never with membranous extensions..... 27

27(30) Male cerci straight..... 28

28(29) Dorsal aedeagal lobes divergent, lateral strongly truncate, connected by a thin membrane..... Tenerife (La Palma).. A. brunneri Krauss

29(28) Dorsal aedeagal lobes parallel, laterally rounded, not connected by a thin membrane.... (Lanzarote). A. lancerottensis Holzapfel

30(27) Male cerci distinctly incurved..... (Fuerteventura). A. fuerteventurae Holzapfel

31(16) Mesosternal lobes rectangular. CYRTACANTHACRIDINAE . 32

32(33) Pronotum deplanate, median carina distinct, but not elevated; male cercus half again as long as wide; subgenital plate with deeply incised apex..... Schistocerca gregaria (Forskål)

33(32) Pronotum raised, median carina distinctly elevated; male cercus over three times as long as wide; subgenital plate deeply trilobate, with rounded lobes..... Anacridium aegyptium (Linnaeus)

34(15) Prosternal process or collar absent..... 35

35(80) Tegminal intercalary vein, at least in the male, well developed, serrate, forming the file of the stridulatory mechanism, hind wings at least tinted with color, often brightly so..... .....OEDIPODINAE . 36

36(53) Median carinae of the pronotum cut by one (posterior) sulcus only..... 37

37(40) Dorsum of the pronotum marked with a distinct X-shaped pattern; wings always banded.....Oedaleus . 38

38(39) Posterior margin of the pronotum strongly angular..... .....Oedaleus decorus (Germar)

39(38) Posterior margin of the pronotum broadly rounded..... ..... Oedaleus senegalensis (Krauss)

40(37) Dorsum of the pronotum without a distinct X-shaped pattern, or if such a pattern is present, the wings are not banded 41

41(46) Hind wing without fascia..... 42

42(43) Larger, male over 35 mm length from fastigium to tip of caudal femur, female over 45 mm; median carina of the pronotum elevated and cristate. Locusta migratoria (Linnaeus)

43(42) Smaller, male under 24 mm length from the fastigium to tip of caudal femur, female under 32 mm; median carina of the pronotum not elevated..... 44

44(45) Elytra pantherine; dark brown pigmentation of wings extending into the vannal area; the hind tibia bright red essentially along entire length..*Aiolopus strepens* (Latreille)

45(44) Elytra pigmentation usually diffuse, if pantherine, the pattern terminates about one-half way from the elytra base; wings hyaline, occasionally with pale brownish pigmentation on the tip. Hind tibia pale tan, occasionally reddish in the distal half .....*Aiolopus thalassinus* (Fabricius)

46(41) Hind wing with fascia.....47

47(48) Wing disk bright orange.....

.....*Scintharista notabilis notabilis* (Walker)

48(47) Wing disk yellow, greenish-blue or blue....*Oedipoda* . 49

49(50) Wings yellowish with transparent apex .....

.....*Oedipoda fuscocincta* Lucas

50(49) Wings greenish-blue to blue throughout.....51

51(52) Head and pronotum strongly rugose; dark fasciae on wings very broad, more than 5 mm at the widest point.....

.....*Oedipoda canariensis* Krauss

52(51) Head and pronotum rugulose; dark fasciae on wings relatively narrow, less than 5 mm at the widest point.....

.....*Oedipoda caerulescens* (Linnaeus)

53(36) Median carina of the pronotum cut by more than one sulcus.54

54(59) Pronotum as long as or shorter than its width..strongly saddle-shaped.....55

55(56) Wings without a dark fascia, yellow tinted at the base..... ..... Acrotylus longipes (Charpentier)

56(55) Wings with a dark fascia, reddish at the base 57

57(58) Posterior margin of the pronotum subangular; antennae shorter than the head and pronotum together..... ..... Acrotylus insubricus (Scopoli)

58(57) Posterior margin of the pronotum broadly rounded; antennae longer than the head and pronotum together..... ..... Acrotylus patruelis (Herrich-Schaffer)

59(54) Pronotum longer than or much longer than its width..... 60

60(67) Pronotum usually strongly rugose, lateral carinae present, median carina cut by two sulci..... Wernerella . 61

61(64) Wings with a dark fascia..... 62

62(63) Integument smooth-punctate; thorax very hairy; angulation of the terminus of the male supra-anal plate acute; angulation of the distal end of the ventral ovipositor valve deep, less than 100^{o}..... Wernerella sublaevis (I. Bolivar)

63(62) Integument rugose; thorax sparsely haired; angulation of the terminus of the male supra-anal plate obtuse; angulation distal end of the ventral ovipositor valve shallow, greater than 120^{o}..... Wernerella pachecoi (I. Bolivar)

64(61) Wings without a dark fascia..... 65

65(66) Integument rugulose; mesozonal sculpturing lateral to median carina fused, forming a complete, obovate depressed area... ..... Wernerella picteti (Krauss)

66(65) Integument smooth-punctate; mesozonal sculpturing lateral to the median carina discontinuous ....Wernerella sp. (Gran Canaria)

67(60) Pronotum smooth, lateral carinae absent, median carina cut by three sulci.....Sphingonotus . 68

68(73) Wings without a dark fascia..... 69

69(70) Supra-anal plate of the male with two sclerotized triangular lobes, crenulate.Sphingonotus willemsei Mistshenko .(Tenerife)

70(69) Supra-anal plate of male without sclerotized lobes, feebly crenulate..... 71

71(72) Inner face of the hind femur with a single pale band; wings bluish at the base; body moderately long, female less than 30 mm, male less than 22 mm..... ..... Sphingonotus caerulans (Linnaeus)

72(70) Inner face of the hind femur with two pale bands; wings hyaline; body length very long and slender, female more than 35 mm; male more than 27 mm..... .....Sphingonotus rubescens (Walker)

73(68) Wings with a dark fascia.....74

74(75) Wing fascia narrow, pale brown, often interrupted..... ..... Sphingonotus freyi Uvarov

75(74) Wing fascia bold, dark brown, continuous.....76

76(77) Inner face of the hind femur black with two yellow bands..... .....Sphingonotus lucasii Saussure

78(79) Body large, male more than 22 mm long, female more than 30 mm long as measured from the fastigium to the knee of the hind femur; posterior margin of the pronotum very broadly rounded.....Sphingonotus savignyi Saussure

79(78) Body medium, male body length less than 19 mm long, female less than 27 mm; posterior margin of the pronotum obtuse-angulate.....Sphingonotus canariensis (Saussure)

80(35) Tegminal intercalary vein absent, or the vein is weak, irregular and not serrated to form a file; hindwings hyaline..81

81(82) Head in profile strongly acute, eyes nearer to apex than to base, frons strongly oblique; antennae ensiform; hind femora long and narrow, its stridulatory file represented by closely-set rigid tubercles and articulated bristles.....
.....TRUXALINAE . Truxalis nasuta (Linnaeus)

82(81) Head subglobular or obtusely and feebly conical; eyes nearer to the base than to the apex, antennae filiform, or slightly compressed at the basal half, but not widened; hind femur narrow, its stridulatory file with articulated pegs.....
.....GOMPHOCERINAE . 83

83(84) Medium size, female more than 25 mm, male more than 22 mm; frons barely oblique, almost vertical; lateral carinae of the pronotum strongly incurved forming a sharp X pattern; ovipositor without external lateral projection.....
.....Dociostaurus maroccanus (Thunberg)

84(83) Small size, female less than 20 mm, male less than 15 mm; frons distinctly oblique; lateral carinae of the pronotum incurved, often forming a weak X-pattern; ovipositor with external lateral projection..... 85

85(84) Elytra and wings terminating at or barely exceeding the knee of the hind femur; arolium large; epiphallus with a wide bridge, narrow ancorae and large, trilobate lophi..... .....Omocestus simonyi (Krauss)

86(85) Elytra and wings well surpassing the knee of the hind femur; arolium small; epiphallus with a narrow bridge, short ancorae and bilobate lophi ..... Stenohippus bonneti (I. Bolivar)

SUMMARY OF SPECIES OF ACRIDOIDEA

Family: Pamphagidae
Subfamily: Pamphaginae
Species on the Canary Islands: Acrostira bellamyi (Uvarov, 1922)
Purpuraria erna (Enderlein, 1929)

The genera Acrostira (Uvarov, 1922) and Purpuraria (Enderlein, 1929) are members of the Pamphaginae. Members of this subfamily have greatly reduced or absent elytra and wings. The species are mainly African, but some forms penetrate southern Europe and western Asia. The Pamphaginae are usually high elevation forms, although Chopard (1943) states that a few are desert dwellers.

Two female specimens collected on Gran Canaria in February, 1922, were described that year by Uvarov as Orchamus bellamyi n. sp. Orchamus at that time was considered to be an eastern Mediterranean genus, with five previously known species occurring in Syria, Palestine, Crete and Cyprus. Although O. bellamyi did not agree closely with all the generic characters ascribed to Orchamus, Uvarov believed it to be much more closely allied to that eastern assemblage than to any of the Pamphaginae of northwestern Africa or Spain.

In 1958, however, Orchamus Stål 1876 was shown by Dirsh to be generically inseparable from Acinipe Rambur 1838, which until then had included only a group of species occurring around the western Mediterranean in southern Europe and northern Africa. It is therefore reasonable to assume that the Canarian species is much more closely

related to the adjacent mainland forms than Uvarov maintained.

It is interesting in this regard to note that many elements of the Canarian vascular flora are introduced or are natural immigrants from the Mediterranean region (Lems, 1960). For example, the Canarian species of Ranunculaceae are all reported to be Mediterranean in origin.[2] Similarly, the Rosaceae, Scrophulariaceae, Umbelliferae and many other Angiosperm families have largely Mediterranean affinities.

Another endemic Canary Island pamphagid, Purpuraria erna, was described by Enderlein in 1929, and in the same publication he erected the monotypic genus Acrostira for Uvarov's Orchamus bellamyi.

Acrostira and Purpuraria are extremely similar, although Acrostira is larger in both sexes, has 15 segmented antennae rather than the 11 or 12 segmented ones as in Purpuraria, and exhibits differences in the extent of wing reduction. Female Acrostira are apterous; similar structures in the male are vestigial. Elytra and wings are vestigial in female Purpuraria and these narrowly elongate-lobiform structures reach the first abdominal segment in the male.

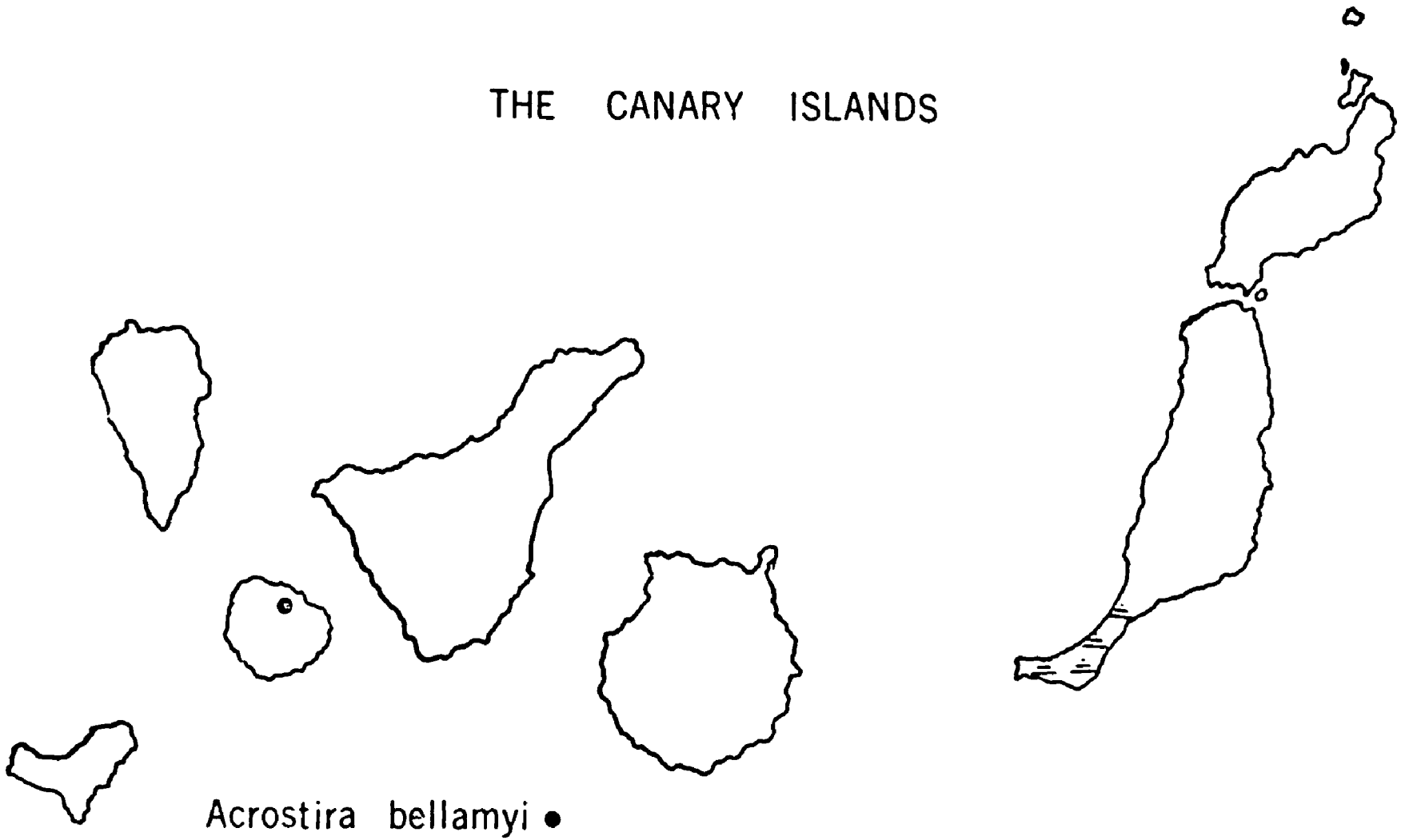
Ecologically, both Acrostira and Purpuraria are montane forms. Acrostira is endemic to Hermigua, a rigorous dissected area in the heart of the heath zone of northern Gomera (Map 2). Purpuraria is known only from the mountain ridge, Jandia, on Fuerteventura, a small,

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[2] Lems (1960) questions the geographic affinities of the endemic Canarian Ranunculus cortusaefolius Willd., although a form on the island of Crete is said to be closely related (Lowe, 1857).

MAP 2. Distribution of the Pamphaginae in the Canary Islands.

DISTRIBUTION OF THE PAMPHAGINAE IN THE CANARY ISLANDS



Acrostira bellamyi •

Purpuraria erna =

steep range rising abruptly 2400 feet from the Atlantic Ocean on the northwestern coast of the island (Map 2).

Family: Pyrgomorphidae
Species on the Canary Islands: Pyrgomorpha cognata Krauss 1877
Pyrgomorpha tereticornis (Brullé 1840)

Pyrgomorpha tereticornis Brullé is an endemic of the Canary and Cape Verde Islands. The genus, however, is mainly African, with several species extending into southern Europe and southwestern Asia (Johnston, 1956; 1968). In Chopard's review of the Chevalier expedition to the Cape Verdes (1936), he reports that P. tereticornis very closely resembles P. cognata, differing from the latter mainly in characteristics of the pronotum. P. cognata is recorded from the whole of Africa, as well as southwestern Asia, and the category seems to be a general catch-all for a wide assemblage of different forms.[3]

The presence of P. cognata on the Canaries is in some question. In 1960, Gardner recorded this species from two localities on the islands, Puerto de la Cruz, Tenerife, and Maspalomas, Gran Canaria. Maspalomas is only a few kilometers from the spot where I collected P. tereticornis. Since I have not seen Gardner's material, I have mapped P. cognata as recorded, but with reservation (Map 3).

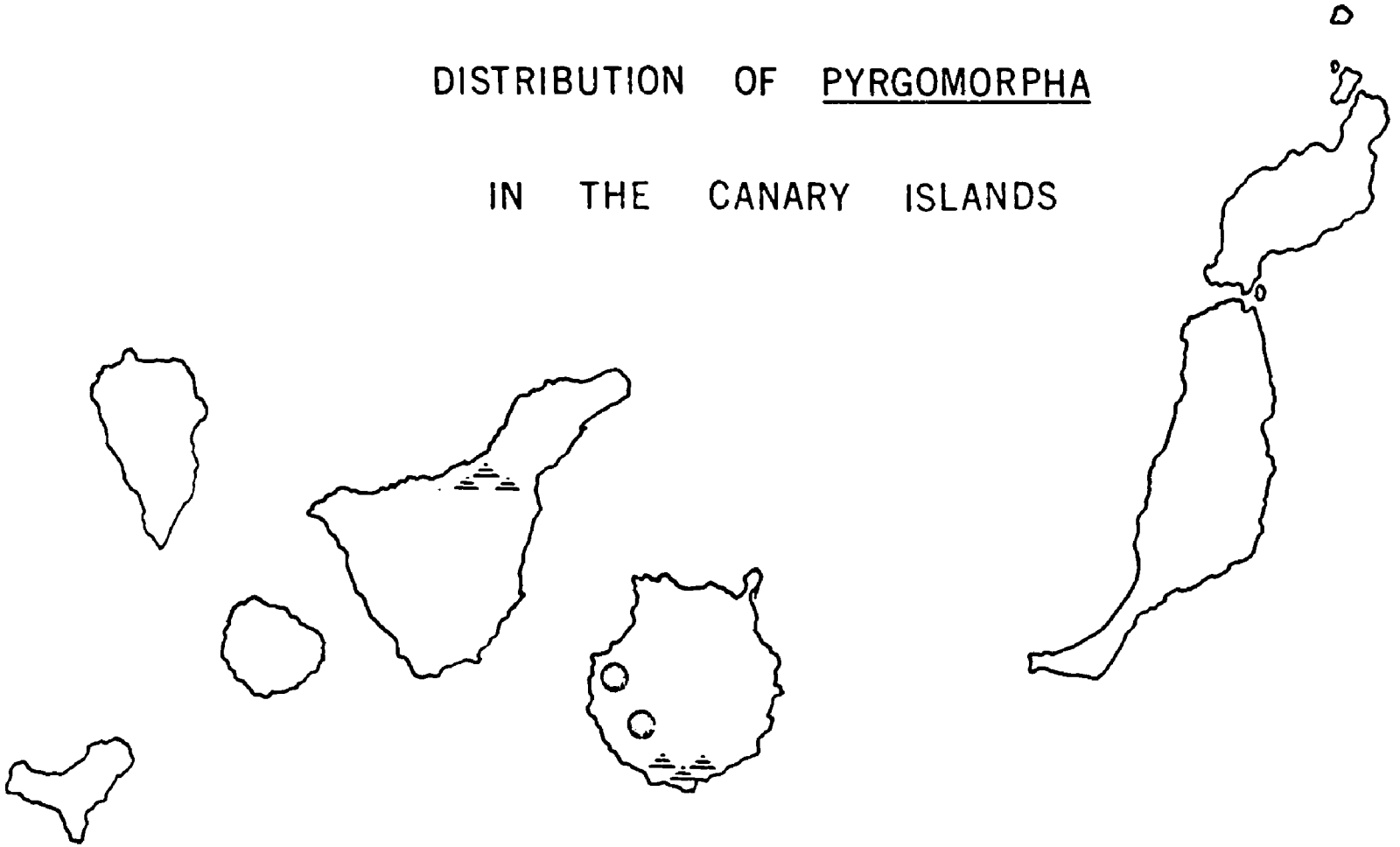
Little is known about the ecology of P. tereticornis. I found the species in two localities on Gran Canaria, San Nicolas, located on the western coast at 50 meters, and Mogan, located in the dry south-

[3] Dirsh (1965) indicates that this species is often misdetermined.

MAP 3. Distribution of Pyrgomorpha in the Canary Islands.

DISTRIBUTION OF PYRGOMORPHA

IN THE CANARY ISLANDS



P. tereticornis

P. cognata

west portion of the island at 770 meters.

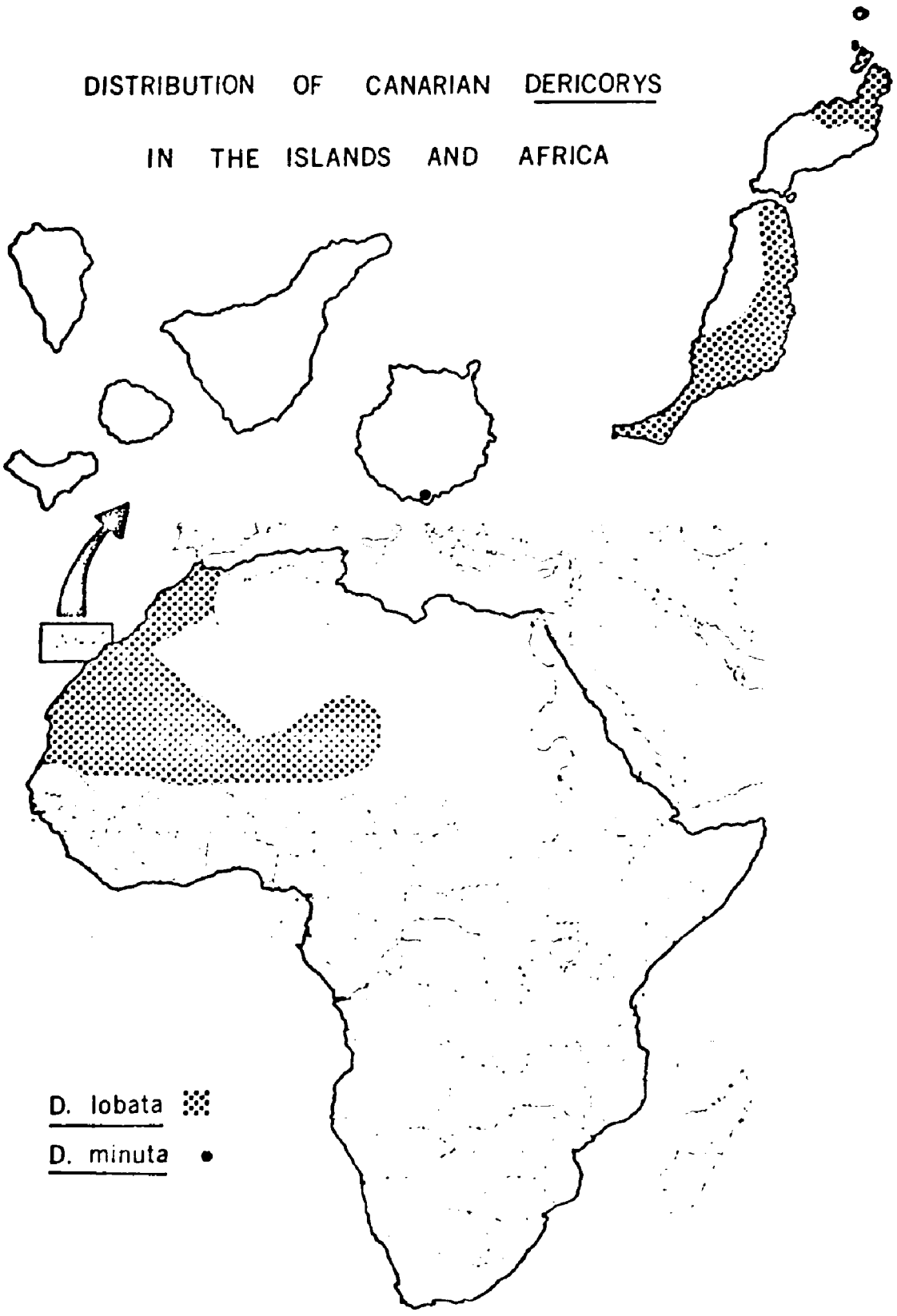
Adults and nymphs were abundant at both grassy-weedy localities in June. The genus as a whole is found in arid habitats; some Moroccan species extend into the dry montane deserts of North Africa (Chopard, 1943).

Family: Acrididae
Subfamily: Dericorythinae
Species on the Canary Islands: Dericorys lobata lobata Brullé 1840
Dericorys lobata luteipes Uvarov 1938
Dericorys minuta Chopard 1954

The genus Dericorys was described in 1838 by Serville. The taxon represents a group of seven, mainly African species, of which two, D. albidula Serville 1838 and D. millierei Finot and Bonnet 1884 are reported from southwestern Asia (Johnston, 1956; 1965). Dericorys, as a genus, occurs north of the equator and is found from the Canary Islands to Eritrea and Somaliland on the east coast of Africa. In the Canary Islands, it occurs on Lanzarote, Fuerteventura, Gran Canaria and on smaller island outcroppings of Lanzarote: Graciosa, the tiny Montaña Clara and Alegranza.

Two species of Dericorys are known from the Canaries: D. lobata Brulle 1840, which occurs also on the Moroccan coast, and D. minuta Chopard 1954, recorded only from Gran Canaria (Map 4). In 1938 Uvarov distinguished three subspecies of lobata, based primarily on differences in head sculpture and in coloration of the hind tibiae of the female. These are: l. lobata on Graciosa, with nearly smooth

MAP 4. Distribution of Canarian Dericorys in the Islands and Africa.


DISTRIBUTION OF CANARIAN DERICORYS
IN THE ISLANDS AND AFRICA
D. lobata
D. minuta

head and hind tibia dirty-red with bright yellow base; I. luteipes on Fuerteventura, with nearly smooth head and hind tibia uniformly honey-colored; and I. bolivari on the Moroccan mainland, with distinctly punctate and rugose head and hind tibia yellow. Material of this species which I collected in the Playa Famara- La Caleta region of northwestern Lanzarote is inseparable from material of D. lobata from nearby Graciosa. The other species, D. minuta, is smaller and slightly shorter-winged than lobata.

My morphological studies of Canary Island series of Dericorys lobata tend to confirm the reality of Uvarov's subspecies, although the difference in tibial coloration upon which he based the separation of I. lobata and I. luteipes is less clear-cut than he thought; the red and yellow coloration supposedly characteristic of the former is also common in I. luteipes. There are, however, other significant differences between these two subspecies, as described below.

In all the Canarian populations, the dorsum of the pronotum is distinctly elevated on the prozona and posterior part of the metazona, with a "valley" between. Measurement of the height of these raised parts above the "valley" and calculation of the ratio of the anterior to the posterior showed that in I. lobata the two are about equal in height, whereas in I. luteipes the anterior elevation is slightly higher than the posterior (Table 1).

The pigmentation of the tubercles in both sexes was also found to differ in the populations on different islands. In the series of I.

TABLE 1. Relationship between height of metazonal crest and prozonal crest (M/P) as measured from the "valley" in male Dericorys.

Island	Locality	Prozonal crest in mm	Metazonal crest in mm	M/P
Fuerteventura	Correlejos	3.2	2.2	.62
	Rosario	3.0	2.0	.67
	Rosario	2.5	1.7	.68
	Rosario	2.2	1.7	.79
	Rosario	2.3	1.8	.80
	Cofete	2.5	2.0	.80
	Rosario	2.2	1.8	.82
	Mal Nombre	2.9	2.5	.86
	Mal Nombre	3.0	2.7	.90
	Mal Nombre	3.0	2.7	.90
	Gran Valle	2.9	2.7	.91
	Mal Nombre	3.0	2.8	.93
		$\bar{X}$ = 2.7	$\bar{X}$ = 2.2	$\bar{X}$ = .81
		σ = .2	σ = .2	
Lanzarote	La Caleta	2.1	2.4	1.10
	La Caleta	2.2	2.3	1.00
	Playa Fanara	2.2	2.3	1.00
		$\bar{X}$ = 2.2	$\bar{X}$ = 2.3	$\bar{X}$ = 1.03
		σ = .1	σ = .1	
Gran Canaria	Maspalomas	0.8	0.6	.75

lobata from Lanzarote and Graciosa, the raised points on the surface are conspicuously and consistently black, even along the ridges of the hind femur; in series of L. luteipes from Fuerteventura they are usually pale yellowish and only rarely somewhat darkened. In D. minuta the tubercles are only rarely pigmented.

Initially it was thought that the Lanzarotean specimens had more tubercles per unit area than those from Fuerteventura, but counts of the number of tubercles per mm^2 on the side of the pronotum (Table 2) show no statistical difference between these two populations. In D. minuta there are more tubercles per mm^2 on the side of the pronotum than in D. lobata, but if allowance is made for the smaller body and tubercle size (the pronotal length is about 0.6 times that of lobata) the number of tubercles per unit area is about the same in the two species ($14/mm^2$).

Figures 1 and 2 illustrate size relations in Dericorys lobata on the Canary Islands. The smallest specimens came from Lanzarote and Graciosa, in the most northern part of the species range. On Fuerteventura, there is a general trend towards increase in size as one moves south. A single exception is one large male from Correlejo in the most northern part of the island. In general, the total body length of males from Playa Blanca and Puerto Rosario, in the north, cluster around 21 mm. The same measurement from the southern localities of Boco mal Nombre and Gran Valle is 22 mm, or over. North-south size trends are not discernible in female lobata.

TABLE 2. Number of tubercles per unit area in male Dericorys*

Dericorys from Fuerteventura	Dericorys from Lanzarote	Dericorys from Gran Canaria
17	14	20
16	16	27
13	11	
14	15	$\bar{X}$ = 24
13	14	σ = 3.8
16	16	
9	11	
14	12	
15		
11	$\bar{X}$ = 14	
10	σ = 2.0	
9		
13		
15		
14		
12		
15		
15		
9		
11		
$\bar{X}$ = 13		
σ = 2.6		

* Number of tubercles counted in 1 mm square areas on the ventro-posterior margin of the pronotum. One count was made on each side of the pronotum of a given specimen.

FIGURE 1. Size of Dericorys lobata males from Lanzarote and Fuerteventura. Squares: males from Lanzarote. Circles: males from Fuerteventura.

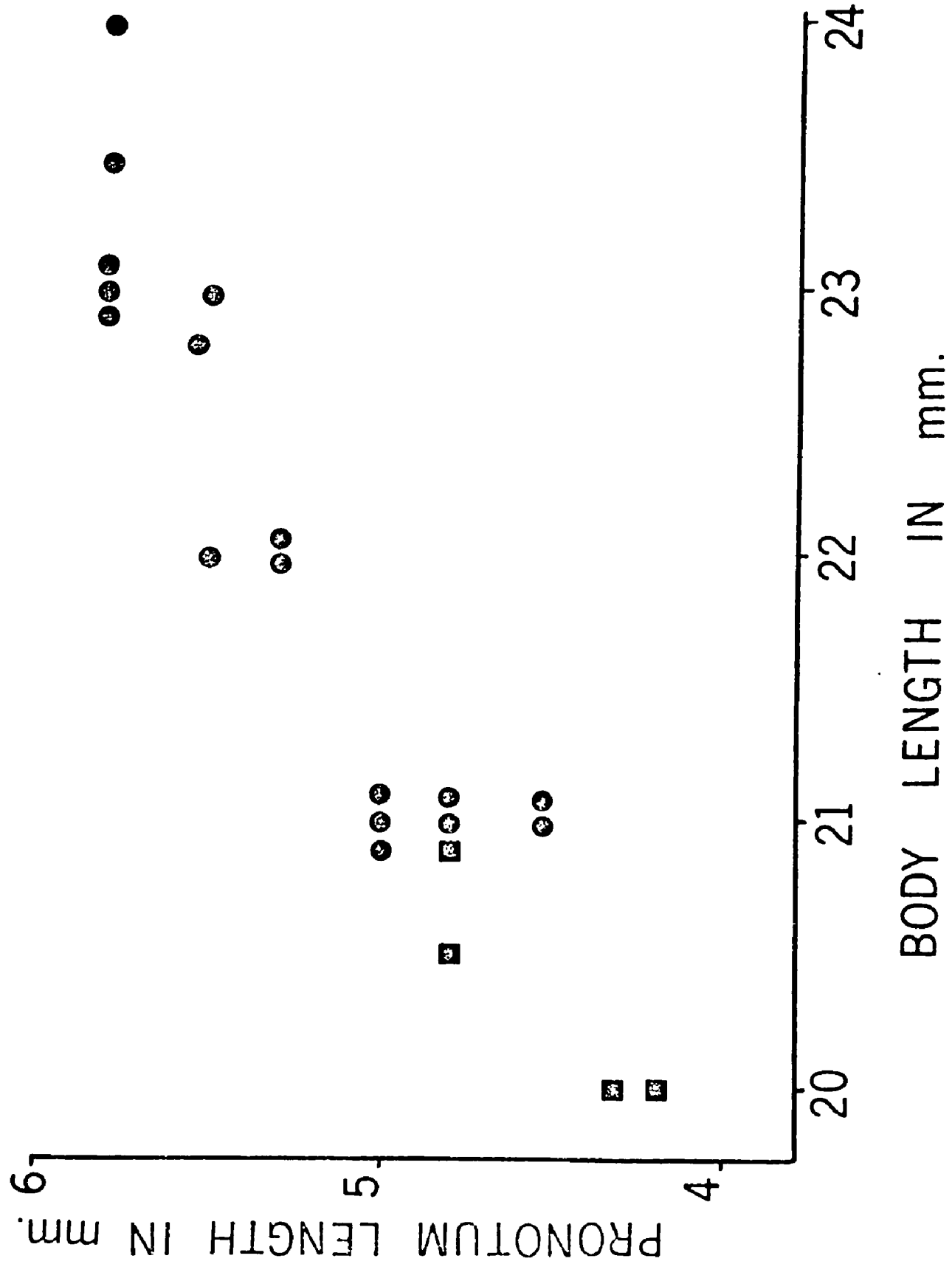
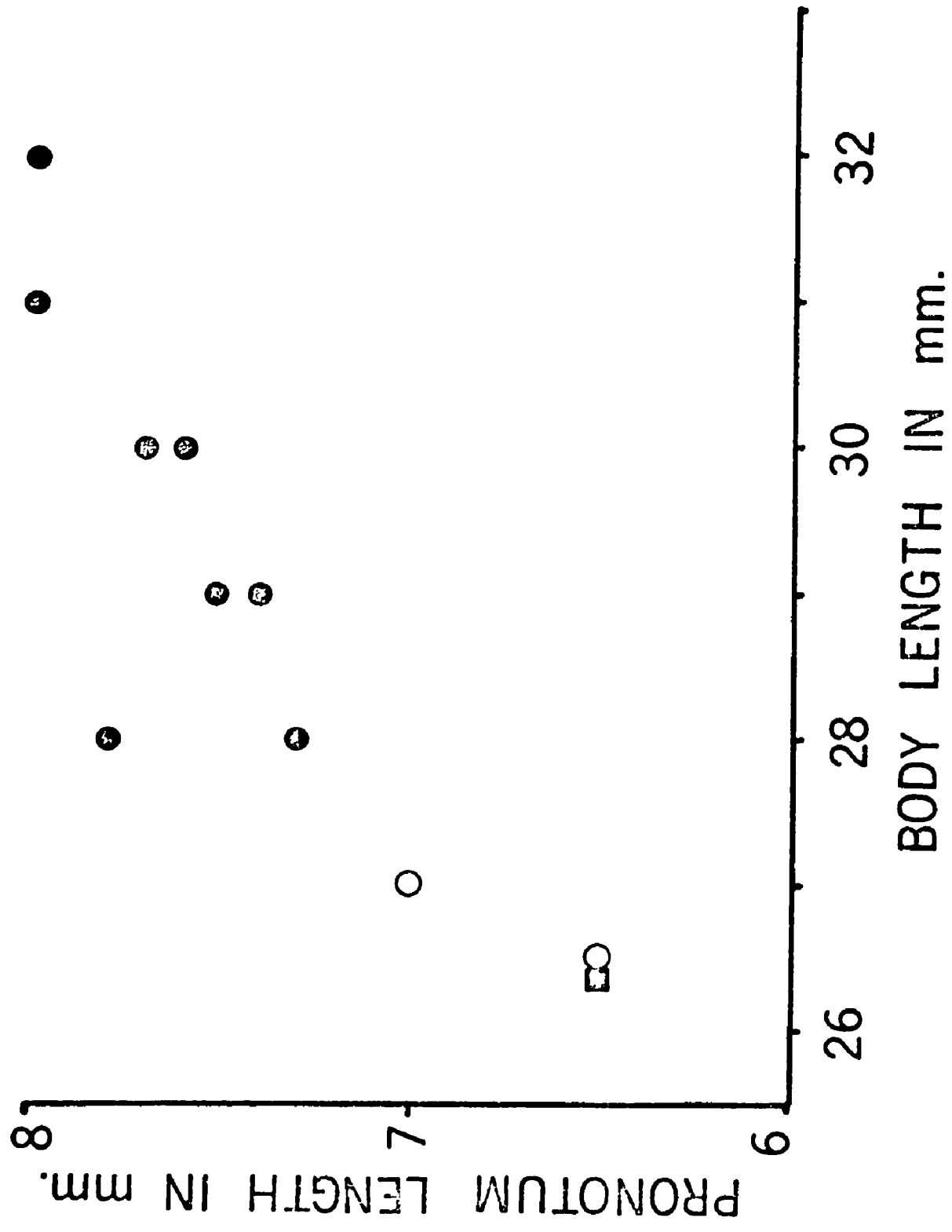

PRONOTUM LENGTH IN mm.
6
5
4
20
21
22
23
24
BODY LENGTH IN mm.

FIGURE 2. Size of Dericorys lobata females from Lanzarote, Graciosa and Fuerteventura. Open circles: females from Graciosa. Closed circles: females from Fuerteventura. Square: female from Lanzarote.


PRONOTUM LENGTH IN mm.
8
7
6
BODY LENGTH IN mm.
26
28
30
32

The question of latitude and size is an important one because D. minuta, the smallest of the Dericorythinae on the Islands, has the most southerly distribution (Map 4). Based on size alone, one might suggest that D. minuta was derived from Lanzarotean lobata. However, the locations of the islands relative to one another, and similarities in pronotal characters with Fuerteventuran D. lobata throw doubt on this hypothesis.

All specimens available (47 ♂, 9 ♀ from Fuerteventura, 2 ♀ from Graciosa, 4 ♂ and 1 ♀ from Lanzarote and 1 male from Gran Canaria) were studied comparatively in many characters including features of the internal and external genitalia of the males, width of the fastigium of the vertex, and position and length of the elytra pigment band in both sexes. No consistent insular differences in these characters were observed.

All specimens taken by me or received on loan were collected in open habitats below 200 meters. Table 3 is a compilation of plant species present at 1965-66 collecting sites of D. lobata on the Canaries. D. minuta was collected in a denuded beach area of Maspalomas, and was therefore not included in this table. D. lobata occurs mainly in semi-desert scrub, particularly those regions with woody chamaephytes and thorned shrubs. Collection areas were characterized by the presence of Launaea spinosa and the small desert annual, Heliotropium erosum. All records in the Canaries of D. lobata adults are for the period from January to May.

TABLE 3. Vegetation at collection sites of Dericorys lobata on Fuerteventura and Lanzarote.

Species	Life Form	Family	Fuerteventura				Lanzarote	
			El Fraile 150 M	Playa Cofete 10 M	Gran Valle 150 M	Bco Mal Nombre 1 M	Corralejo 5 M	Famara 1 M
Atriplex halimus	N	Cheno.				1		
Lycium afrum	N	Solan.	2		1	2		
Suaeda fruticosa	N	Cheno.						2
Zygophyllum fontanesii	N	Zygop.		1			1	
Euphorbia canariensis	SS	Eupho.	2					
Euphorbia handiensis	SS	Eupho.			2			
Aizoon canariense	Ch	Aizoa.	2		2	+		1
Gymnocarpus decandrum	Ch	Caryo.		1	1			
Launaea spinosa	Ch	Compo.	2	1	2	+	+	2
Lotus arabicus	Ch	Legum.	1	1			+	
Polycarpae nivea	Ch	Caryo.		2		+	1	1
Plantago sericea	H	Plant.	+					
Euphorbia paralias	G	Eupho.		+			1	2
Mesembryanthemum crystallinum	G	Aizoa.	1		+	2	+	
Mesembryanthemum nodiflorum	G	Aizoa.	1		1		1	
Periploca laevigata	Li	Asclep.	+					
Echium plantagineum	T2	Borag.	+		1			

TABLE 3. (Continued)

Atractylus cancellata	Th	Compo.	+					
Cakile maritima	Th	Cruci.					2	
Erodium chium	Th	Geran.	+					1
Heliotropium erosum	Th	Borag.	+	1	1	1	1	1
Lithospermum apulum	Th	Borag.				1		
Matthiola bolleana	Th	Cruci.	+					

Family: Acrididae
Subfamily: Calliptaminae
Species on the Canary Islands: Calliptamus barbarus barbarus (Costa 1836)
Calliptamus plebeius (Walker 1870)

The genus Calliptamus was recently reviewed by Jago (1963). Four species have been reported from the Canary Islands: C. plebeius by Walker (1870), C. italicus by Brullé (1840), C. madeirae by Chopard (1954), and C. barbarus barbarus by Bormans (1884). Jago, however, concludes that only the endemic C. plebeius is found on the Canaries.

The 210 individuals of Calliptamus from the five western islands of the archipelago collected during my recent trip to the Islands all proved to belong to C. plebeius (Map 5, Table 4). However, 7 male and 3 female specimens from Lanzarote in the collection of the British Museum were definitely not this species.[4] Comparison of the internal genitalia of the males from Lanzarote with the copulatory morphology of specimens of Calliptamus barbarus barbarus from the Willemse collection, indicated that the material in question is referable to that subspecies. Although madeirae approaches barbarus in many characters, the unique arch of the cingulum of madeirae males rules out the possibility that the Lanzarotean material belongs to that species.

[4] The difference between C. plebeius and the three other species of Calliptamus reported from the Canary Islands may be determined superficially by observing the coloration of the hind wings. In plebeius they are without color or greyish; in the other species they are bright pink.

MAP 5. Distribution of Canarian Calliptamus in the Islands and Africa.

DISTRIBUTION OF CANARIAN CALLIPTAMUS

IN THE ISLANDS AND AFRICA

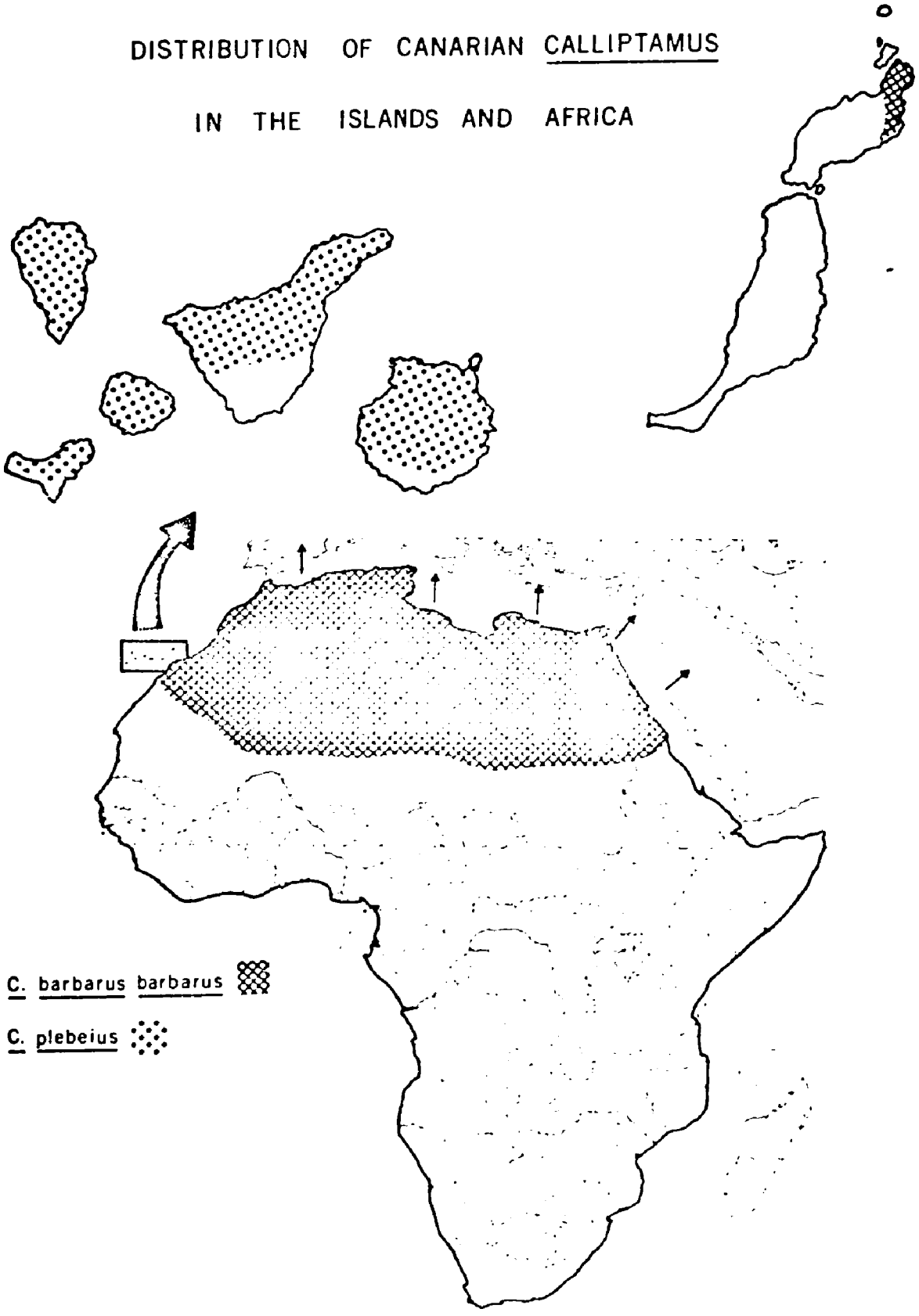


TABLE 4. Vegetation at collection sites of Calliptamus plebeius on Tenerife.

Plant species	Life Form	Family	San Andrés	Trail to Masca 850 M	Open mixed heath at 900M-above Buena-vista	Ucanca-Cañadas-2100M
Arbutus canariensis	M	Erica.			1	
Ilex canariensis	M	Aquif.			1	
Laurus canariensis	M	Laura.			+	
Myrica faya	M	Myric.			1	
Notelaea excelsa	M	Oleac.			1	
Viburnum rugosum	M	Capri.			+	
Aeonium haworthii	N	Crass.			+	
Aeonium urbicum	N	Crass.		1		
Asparagus scoparius	N	Lilia.		+		
Carlina salicifolia	N	Compo.		1		
Cistus monspeliensis	N	Cista			1	
Cistus symphytifolius	N	Cista.			1	
Echium leucophaeum	N	Borag.	1			
Echium strictum	N	Borag.			1	
Erica arborea	N	Erica.			2	
Euphorbia atropurpuria	N	Eupho.		+		
Euphorbia canariensis	N	Eupho.		1		
Euphorbia regis-jubae	N	Eupho.		+		
Hypericam canariensis	N	Hyper.			1	
Hypericum reflexum	N	Hyper.		+	1	
Kleinia neriifolia	N	Compo.		1		
Leucophae massoniana	N	Labia.	+			

TABLE 4. (Continued)

Lytanthus salicinus	N	Globu.			1	
Retama monosperma	N	Legum.		1		
Sonchus leptocephalus	N	Compo.		+		
Spartocytisus nubigenus	N	Legum.				2
Aeonium sedifolium	Ch	Grass.		2		
Bromus sp.	Ch	Grami.				1
Chrysanthemum anethifol.	Ch	Compo.				1
Dicheranthus plocamoides	Ch	Caryo.		1		
Echium bourgeauanum	Ch	Borag.				1
Lavandula pinnata	Ch	Labia.		2		
Lotus campylocladus	Ch	Legum.				+
Lotus mascaensis	Ch	Legum.		+		
Nepeta teydea	Ch	Labia.				1
Phyllis viscosa	Ch	Rubia.		1	1	
Polygonum serrulatum	Ch	Polyg.	1			
Tolpis webbi	Ch	Compo.				+
Agrostis stolonifera	H	Grami.	1			
Andropogon hirtus	H	Grami.		1		
Antirrhium majus	H	Scrop.	1			
Pennisetum sp.	H	Grami.	+			
Pterocephalus lasiosperm	T2	Dipsa.				2
Datura stramonium	Th	Polyg.	1			
Eragrostis sp.	Th	Grami.	1			
Lamarckia aurea	Th	Grami.	+			

A distinctive difference between b. barbarus from the Canaries and 24 male and 24 female specimens of the same subspecies from Yugoslavia and France held in the Willemse collection is that in all cases the elytra and wings well surpass the knee of the hind femur in the former. In the continental material, the elytra and wings always terminate at or barely exceed the knee of the hind femur.

According to Jago (op. cit.), C. barbarus barbarus occupies almost every dry, Mediterranean or semi-desert region and steppe of the Palearctic. The subspecies is widespread in North Africa and extends into southwestern Asia and Europe (Map 5). On the Canary Islands it may best be described as local. Haria, Lanzarote, is a sparsely vegetated semi-desert region, typical of that described by Jago.

Calliptamus plebeius, found on all five of the western islands, is endemic to the Canaries. It may be distinguished from other Calliptamus species of the genus by the distinctive shape of the male cercus, which has a very broad upper lobe and weak and divergent lower lobes, by the very membranous male genitalia which hide the penis vales from above, and by the clear to grey hind wings. When compared with other Calliptaminae, C. plebeius most closely resembles C. barbarus barbarus, and Jago suggests that C. plebeius is derived from North African representatives of this group.

On the Canaries, C. plebeius is found from 150 to 2200 meters, and is one of only three species that occurs in all vegetation

belts above and including the xerophytic zone (Table 17). Table 4 indicates its presence in a wide variety of habitats, confirming its plastic ecological valence, if not suggesting a recent origin.

MATERIAL STUDIED. - LA PALMA: Fuencaliente 600 M, 14 ♀, 6 ♂, May; Fuencaliente 300 M, 1 ♀, September; Barranco Alen 400 M, 4 ♀; Volcan San Antonia 654 M, 1 ♀, 2 nymphs, May; El Time 590 M, 1 ♀, 1 ♂, May; Los Roques 2000 M, 1 ♀, May. HIERRO: Cruz de los Humilladeros 1215 M, 1 ♀, September; El Golfo 830 M, 1 ♂, September; Valverde 570 M, 1 ♀, September. GRAN CANARIA: Fataga, 1100 M, 7 ♀, 3 ♂, 1 nymph, June; Mogan 770 M, 1 ♀, 1 ♂, June; Bandama 350 M, 1 ♀, 3 ♂, May; 7 km. east of Tejeda 1400 M, 10 ♀, 2 ♂, May; Roque Nublo 1700 M, 1 ♀, 2 ♂, May; Buen Lugar, 1 nymph, 1 ♀, 4 ♂, June; East of Guia 200 M, 2 ♀, 1 ♂, June; El Risco 1000 M, 2 ♀, 1 ♂, 1 nymph, June; Tazartico 660 M, 3 ♀, June; San Nicolas 150 M, 2 ♀, 2 ♂, 2 nymphs, June; San Bartolomé 750 M, 1 ♀, 1 ♂, 1 nymph, June. GOMERA: Barranco Ville 250 M, 14 ♀, 2 ♂, March; Aruré 800 M, 17 ♀, 5 ♂, 6 nymphs, March; Valle Gran Rey 560 M, 1 ♀, 2 ♂, March; Tagamiche 680 M, 9 nymphs, March. TENERIFE: San Andrés 250 M, 14 ♀, 9 ♂, April; Cañadas 2100 M, 2 ♀, 1 ♂, August; Buena Vista 900 M, 1 ♀, October; Barranco del Infierno 275 M, 1 ♀, May; Barranco del Infierno 220 M, 2 ♀, 1 ♂, August; Castillas 550 M, 1 ♀, April; Barranco Igueste 400 M, 1 ♀, April; Barranco Igueste 180 M, 1 ♀, 1 nymph, April; Chio 800 M, 8 ♀, 6 ♂, 2 nymphs,

May; Santiago-Masca 975 M, 1 ♂, September; Masca 850 M, 9 nymphs, April; Above Raices, 1 ♀, February.

Family: Acrididae
Subfamily: Eyprepocnemidinae
Species on the Canary Islands: Eyprepocnemis cinerea (Blanchard, 1853)

Eyprepocnemis cinerea is endemic to the Canary Islands. Although the locality of the collection was not reported, Blanchard's type is from Tenerife. The first specimens known from Gran Canaria were taken by K. M. Guichard in August 1966 at Maspalomas (BMNH). Maspalomas is an open sandy beach bordering a unique flora including a natural palm oasis and the rare endemic halophyte, Limonium preauxii (Webb). I have stipled the desert region of Tenerife as the likely collection site of cinerea on that island (Map 6).

The genus Eyprepocnemis has been recently revised by Dirsh (1958), who unfortunately did not include cinerea in his study. Uvarov, in his "Notes on the Orthoptera of the British Museum" (1921), indicated a close relationship of this species to E. bandana longipes, found in west and central Africa.

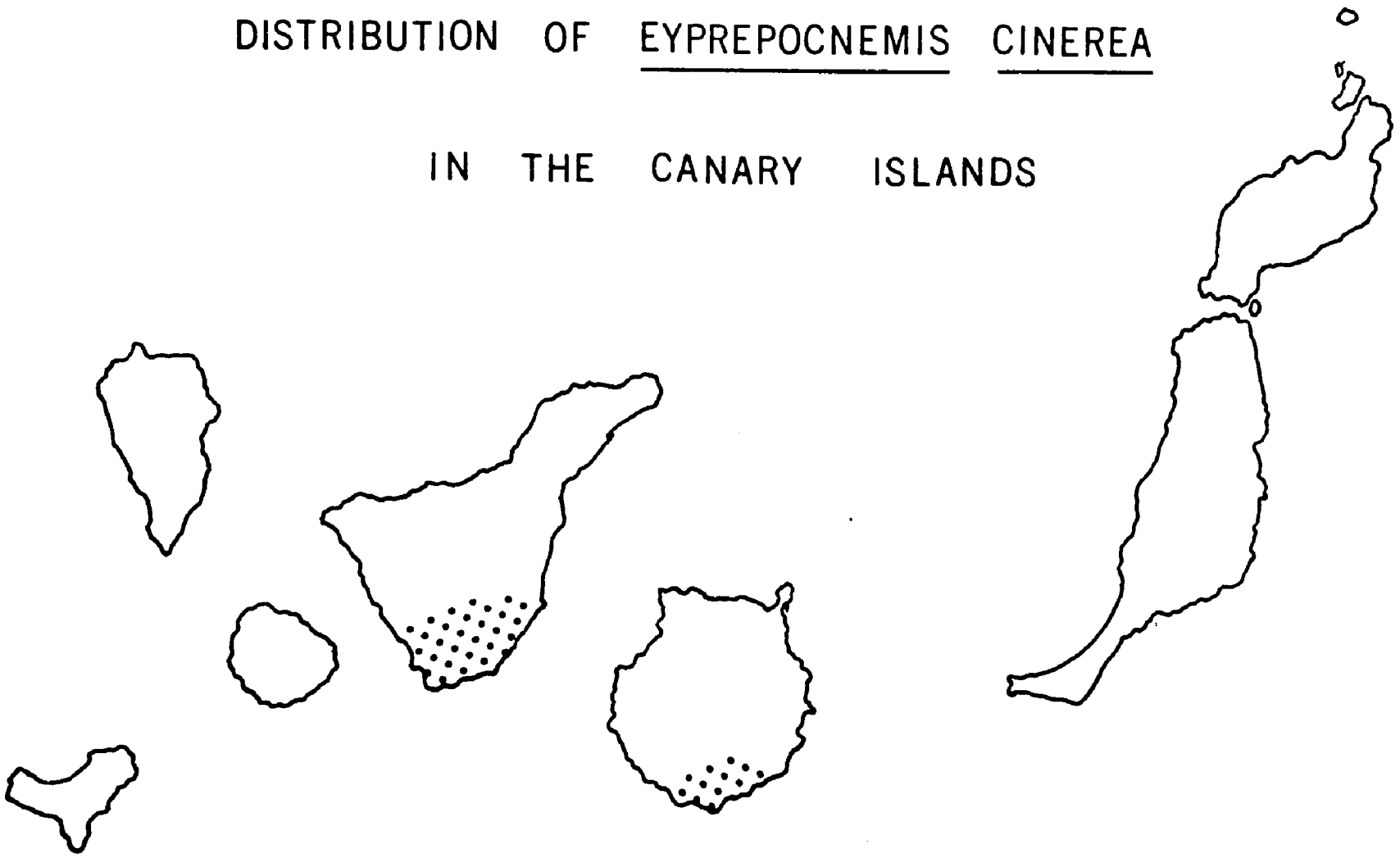
Family: Acrididae
Subfamily: Cyrtacanthacridinae
Genus and species on the Canary Islands: Anacridium aegyptium (Linnaeus 1764)

The distribution of Anacridium includes all of the African continent, and extends into southern Europe, southwestern Asia and

MAP 6. Distribution of Eyprepocnemis cinerea in the Canary Islands.

DISTRIBUTION OF EYPREPOCNEMIS CINEREA

IN THE CANARY ISLANDS



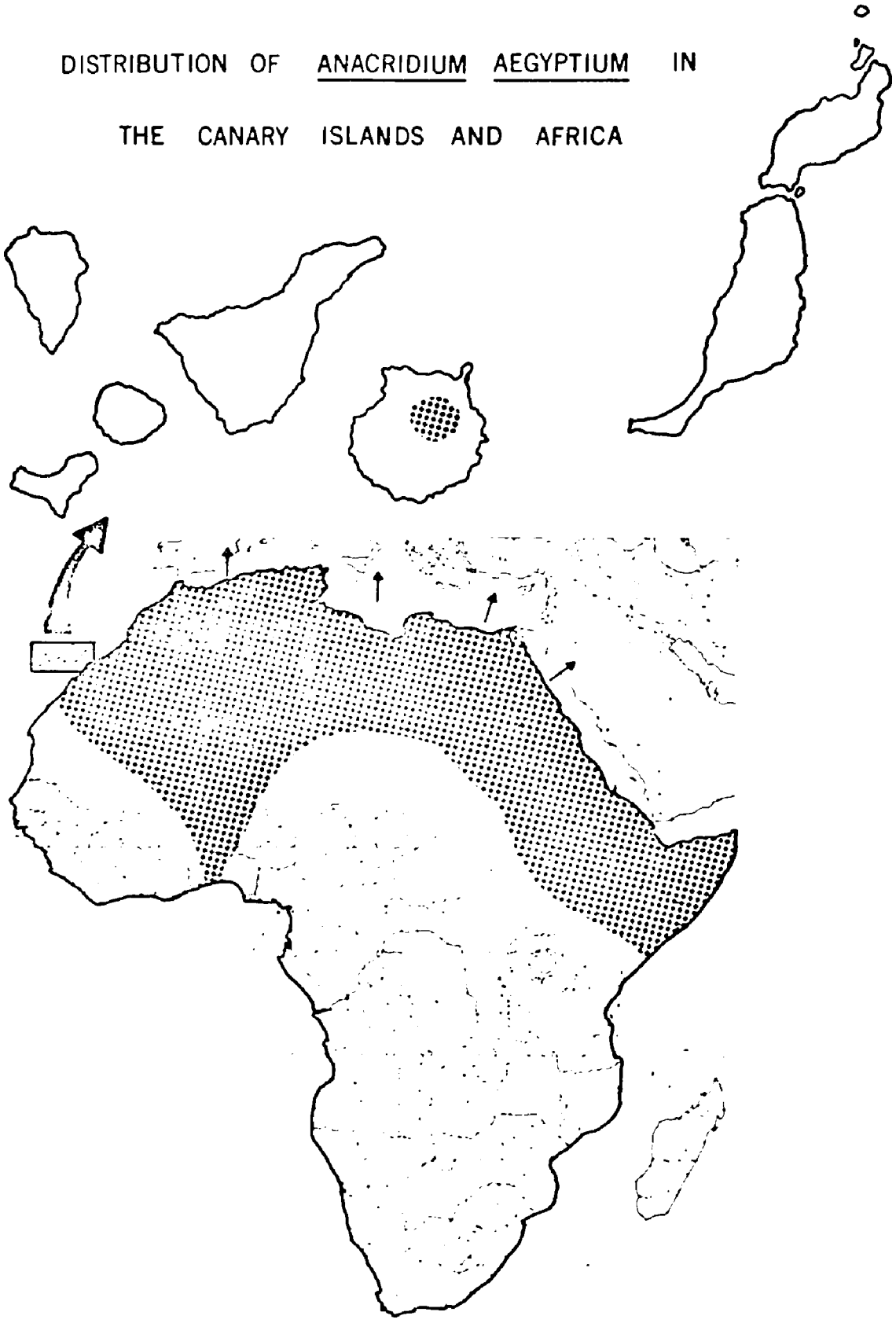
India. However, the distribution of A. aegyptium is mainly Mediterranean; in Africa, it is restricted to coastal lowlands and dry hilly regions in the north, east and west, and to cultivated areas around Saharan oases. In Europe, the species occurs only in the Mediterranean peninsulas, in Mediterranean France, a few valleys in Switzerland, and in Crimea and Caucasus. In western Asia, it is found in lowland areas, occasionally as far north as Iran (Johnston, 1956, 1968).

Although the genus was monographed by Dirsh and Uvarov in 1953, they were unable to locate Canarian specimens or records. The supposed absence of A. aegyptium from the Canaries has long been a mystery, since it is known from Madeira, and two other species in the genus are found in the much more remote Cape Verde Islands (Johnston, 1956, 1968).

The first specimens of aegyptium from the Canaries were recorded by Gardner (1960), from Santa Brigida, Gran Canaria at 400 meters (Map 7). This is a cultivated, hilly populous area in the northeastern portion of the island. This phase locust is mainly a lowland species. It has been reported in a variety of scrubby habitats, including Quercus pubescens in North Africa (Chopard, 1943). It has also been cited as a common inhabitant of tall trees, brambles, rose bushes and vines in a variety of cultivated areas (Volkonsky, 1943).

MAP 7. Distribution of Anacridium aegyptium in the Canary Islands and Africa.

DISTRIBUTION OF ANACRIDIUM AEGYPTIUM IN THE CANARY ISLANDS AND AFRICA



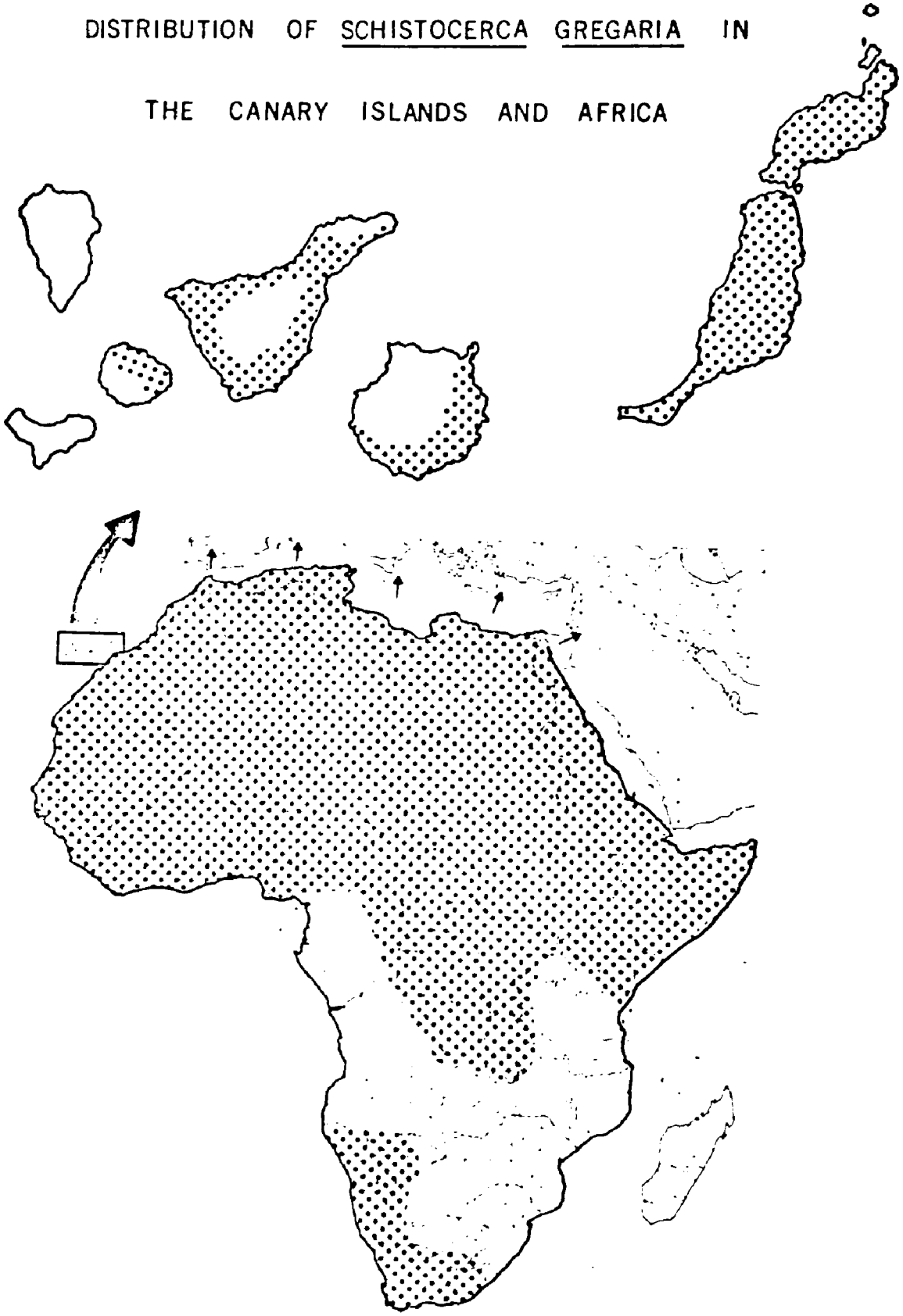
Family: Acrididae
Subfamily: Cyrtacanthacridinae
Genus and species on the Canary Islands: Schistocerca gregaria (Forskål 1775)

Schistocerca gregaria is known from Tenerife, Gomera, Lanzarote, Gran Canaria and Fuerteventura of the Canary Islands and is widespread in Africa, southern Europe and southwestern Asia (Map 8). This large, colorful grasshopper periodically swarms, and exhibits phase polymorphism characterized by changes in coloration and morphology. Much interest has been shown in the biology of this species, both for economic and comparative reasons, particularly since similar phase manifestations have been found in Tettigoniids (Chopard, 1949), Phasmids (Key, 1957), Lepidoptera (Long, 1953; Iwas, 1962) and other Acridoids (Uvarov, 1966).

On the Canaries, I collected two solitary phase adult females of this species on the flat open barrens of the Euphorbia handiense deserts of the Jandia peninsula, Fuerteventura. At the time of collection in early March, 1966, the species was very rare at that locality. I expect that this strong flier is an occasional erratic to all of the Canary Islands, because from time to time, it has been reported in abundance on the more distant archipelagoes, Madeira, the Azores and Cape Verde Islands.

MAP 8. Distribution of Schistocerca gregaria in the Canary Islands and Africa.

DISTRIBUTION OF SCHISTOCERCA GREGARIA IN THE CANARY ISLANDS AND AFRICA



Family: Acrididae
Subfamily: Catantopinae
Species on the Canary Islands:

Arminda (Arminda) brunneri Krauss, 1892
Arminda (Arminda) burri Uvarov, 1935
Arminda (Arminda) fuerteventurae Holzapfel, 1970
Arminda (Arminda) hierroënsis Enderlein, 1930
Arminda (Arminda) lancerottensis Holzapfel, 1970
Arminda (Arminda) latifrons Enderlein, 1930
Arminda (Chopardminda) canariensis Morales Agacino, 1941

Arminda is a genus of wingless grasshoppers endemic to the Canary Islands. Six species of Arminda (Arminda) are known, as well as one closely related species belonging to a distinctive monotypic subgenus, Chopardminda (Map 9). All members of this complex are found in sparsely vegetated open fields below 1000 meters elevation.

A. lancerottensis and A. fuerteventurae are morphologically similar species occurring on the eastern islands of the Canaries. Descriptions of these taxa are now in press (Holzapfel, 1971). Arminda fuerteventurae is a small, golden-tan grasshopper, with known distributions in the central portion of the island of Fuerteventura. A. lancerottensis is endemic to northern Lanzarote. Females of these two species vary widely in body shape, coloration and features of the external genitalia (Figs. 3, 4), and cannot be distinguished on morphological grounds. The males, however, are distinctive. A. lancerottensis differs from fuerteventurae in that 1) the cerci are straight rather than incurved (Figs. 5, 6D), 2) the aedeagal lobes are

MAP 9. Distribution of Arminda and Chopardminda on the Canary Islands. Island and species codes west to east: H = Hierro, A. hierroënsis = open circle; P = La Palma, A. brunneri = closed circle; G = Gomera, A. latifrons = semi-circle; T = Tenerife, A. brunneri = closed circle; A. burri = square; C = Gran Canaria, A. burri = square, Chopardminda canariensis = broken triangle; F = Fuerteventura, A. fuerteventurae = closed triangle; L = Lanzarote, A. lancerottensis = open triangle.

DISTRIBUTION OF ARMINDA AND CHOPARDMINDA IN THE CANARY ISLANDS

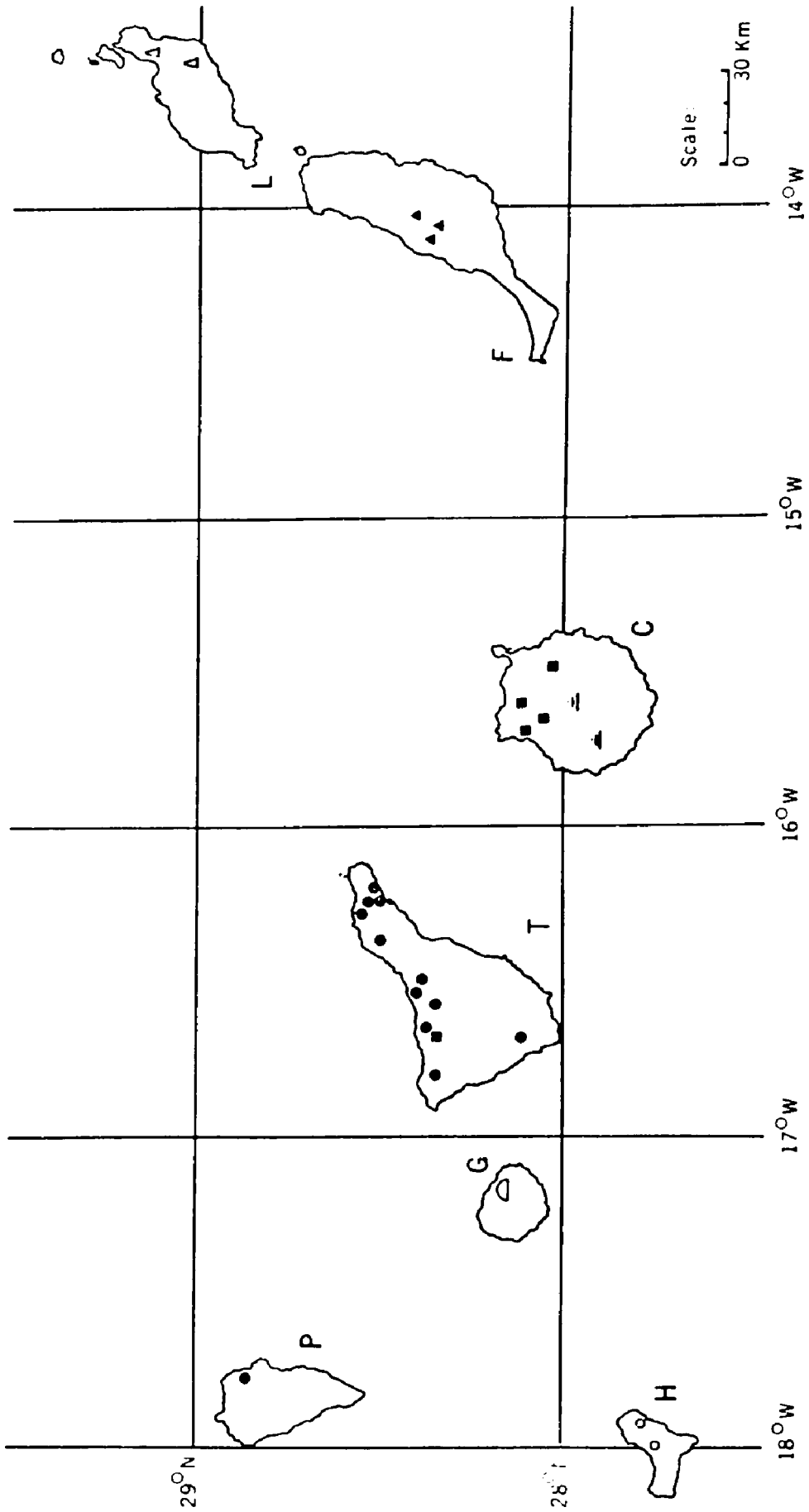


FIGURE 3. Dorsal and lateral views of female Arminda fuerteventurae (A, B) and female Arminda lancerottensis (C, D).

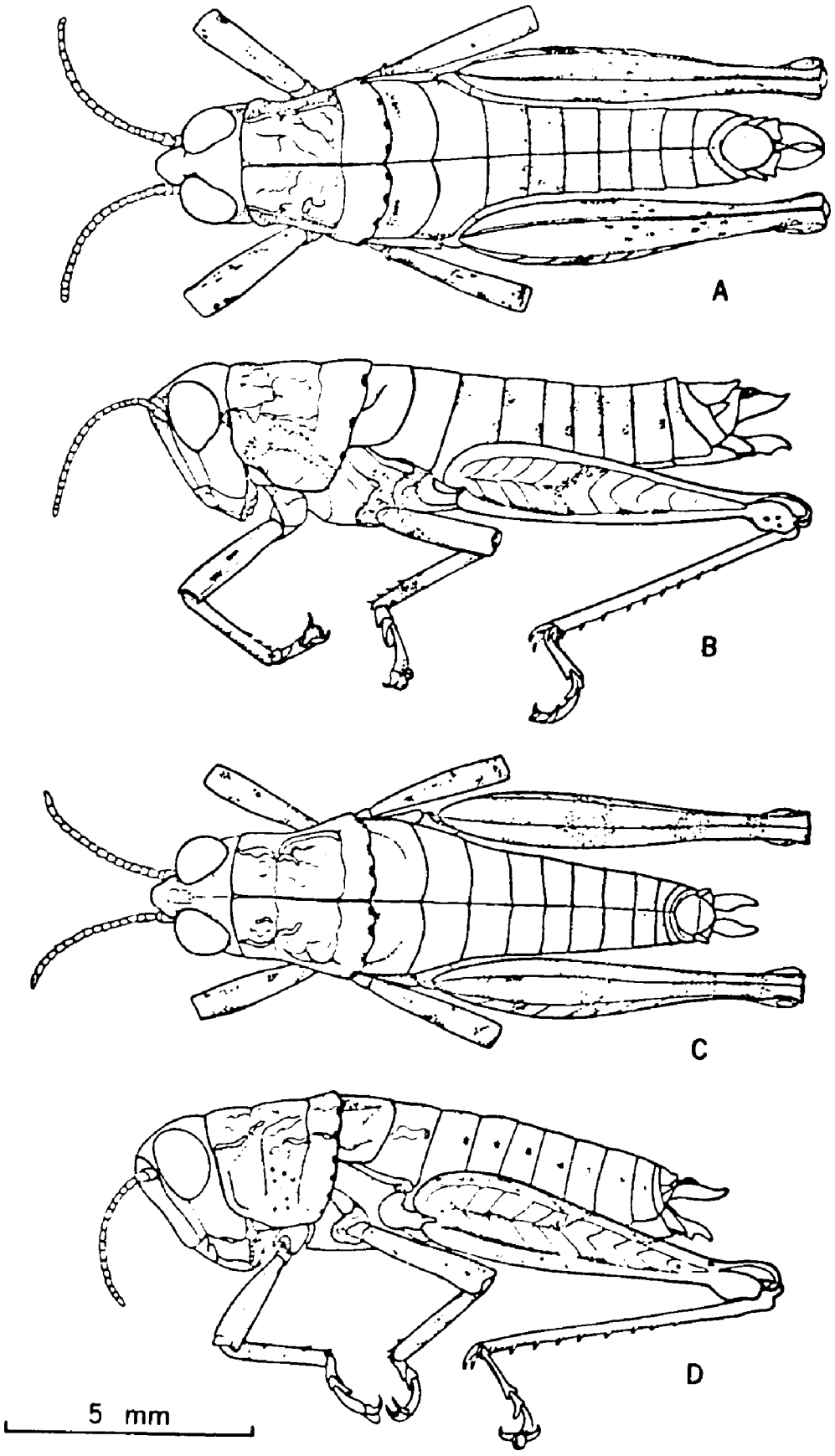

A
B
C
D
5 mm

FIGURE 4. Lateral view of the external genital complex, dorsal view of the supra-anal plate, and ventral view of the subgenital plate of females of Arminda fuerteventurae (A, B, C) and Arminda lancerottensis (D, E, F).

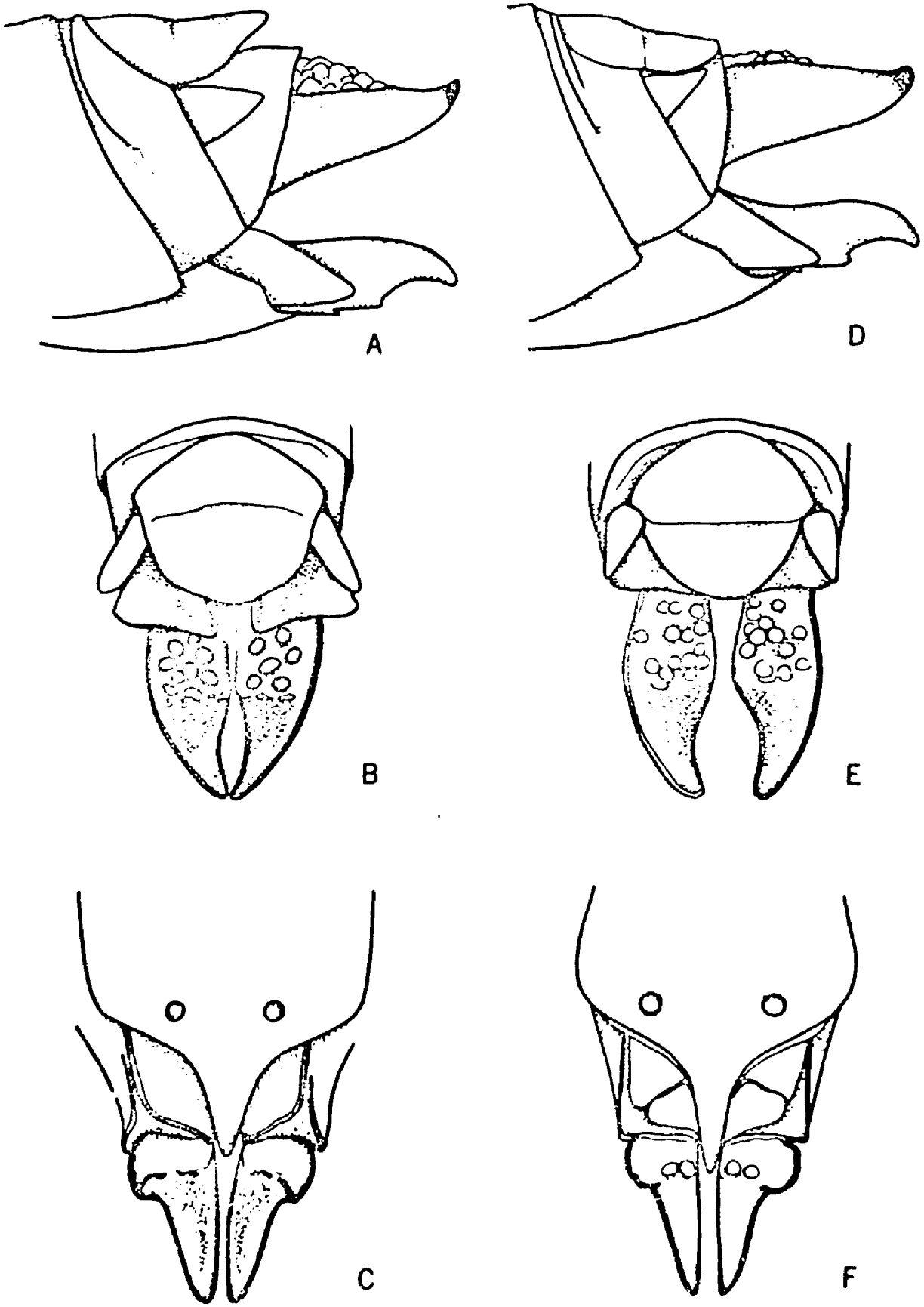

A
D
B
E
C
F

FIGURE 5. Dorsal and lateral views of male Arminda fuerteventurae (A, B) and male Arminda lancerottensis (C, D).

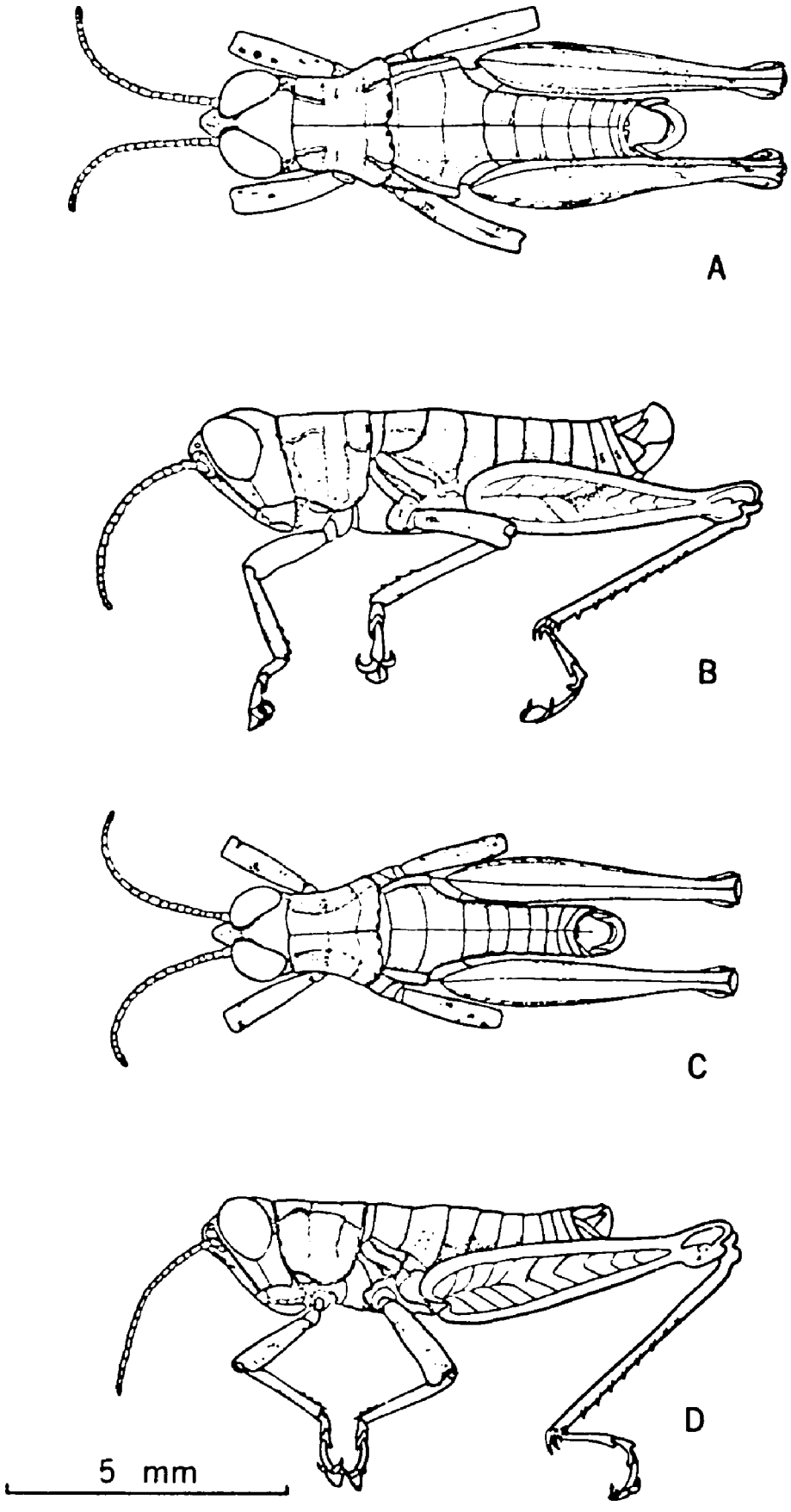
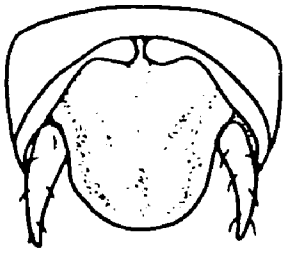
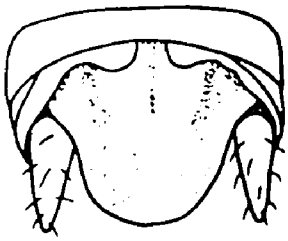

A
B
C
D
5 mm

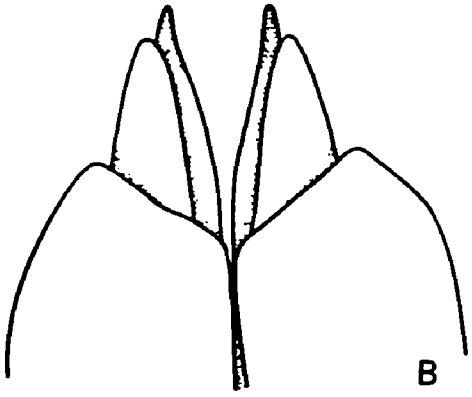
FIGURE 6. Dorsal view of the supra-anal plate and cerci of male A. fuerteventurae (A) and male A. lancerottensis (D). Ventral view and cross section of the dorsal lobes of the aedeagus of A. fuerteventurae (B, C), and A. lancerottensis (E, F). Epiphallus of A. fuerteventurae (G). Ventral view of the dorsal lobes of the aedeagus of A. burri (H) and A. brunneri (I).



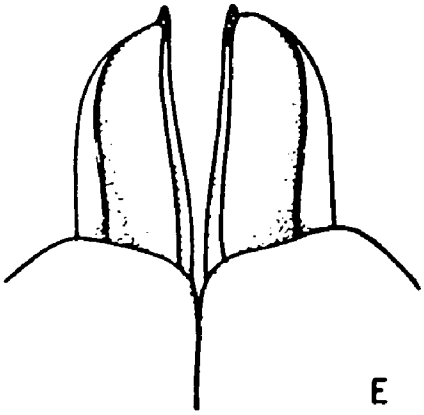
A



D



B



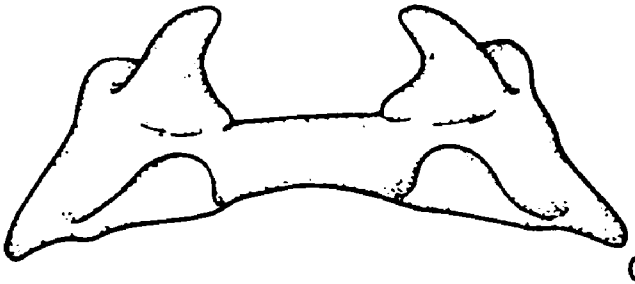
E



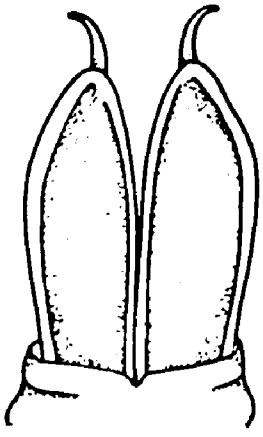
C



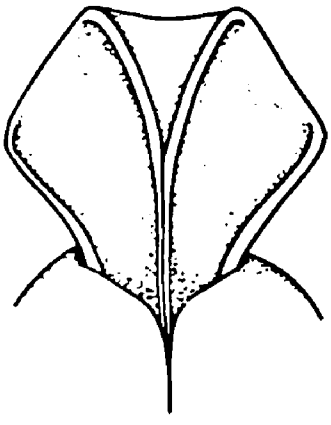
F



G



H



I

laterally truncate instead of broadly acuminate (Fig. 6E), and the aedeagal lobes are J-shaped rather than C-shaped in cross section (Fig. 6 F). General morphology of the two species is illustrated in figures 3 and 5.

A. burri is known from the northern portion of Gran Canaria in scantily vegetated areas, and has one known locality on Tenerife.[5] This species differs from other Armindas in a variety of ways and may easily be distinguished on the basis of larger body size (Table 5), and membranous extensions of the dorsal lobes of the aedeagus (Fig. 6 H).

Three species of Arminda have been reported from Tenerife, A. brunneri, the genotype, A. striatifrons, and A. appenhageni. A. brunneri was described in 1892 by Krauss on the basis of one female specimen collected at San Andrés on the northeastern coast of Tenerife. In 1929, Enderlein described two new species of Arminda appenhageni, also from San Andrés, and A. striatifrons from Guajonge. The localities from which these three species were described lie within 16 km of each other on the Anaga Peninsula in the northernmost corner of the island. All three holotypes are females, which in many grasshopper taxa are notoriously variable and more difficult than males to distinguish. No diagnoses were included in the description of Enderlein's species; the characters noted were general body coloration,

[5] One male specimen collected by K. M. Guichard at La Vega, Tenerife, (BMNH), is indistinguishable from A. burri of Gran Canaria.

TABLE 5. Size range of Arminda determined from the literature and museum specimens (in mm).

		A. brunneri Krauss 1892	A. hierroënsis Enderlein 1930	A. latifrons Enderlein 1930	A. burri Uvarov 1935	A. fuert.	A. lancer.
Body length (Head to end hind femur)	♂	10.8 - 12.5	10.0 - 10.5	----	16.0 - 16.5	9.6 - 10.8	9.8 - 10.3
	♀	14.5 - 19.0	14.3 - 16.3	18.5	21.0 - 24.0	12.1 - 14.8	13.0 - 13.8
Length pronotum	♂	2.2 - 2.6	----	----	2.8 - 3.5	1.6 - 1.9	1.7 - 1.8
	♀	2.8 - 3.9	----	----	4.0 - 5.0	3.0 - 3.1	2.8 - 2.9
Length hind femur	♂	6.3 - 7.7	----	----	8.3 - 9.5	5.0 - 5.8	5.2 - 5.4
	♀	7.3 - 10.5	----	----	11.4 - 12.3	6.8 - 7.5	7.3 - 7.5

interocular distance, shape of the lower ovipositor valve, and morphology of the flagellum of the antenna.

I examined one hundred and nine specimens of Arminda from Tenerife. These were sorted into localities and arranged in east-west order. Few specimens were available from the northwest portion of the island. Size, details of external morphology and internal male genitalia were studied in specimens from each area. The following relationships were observed:

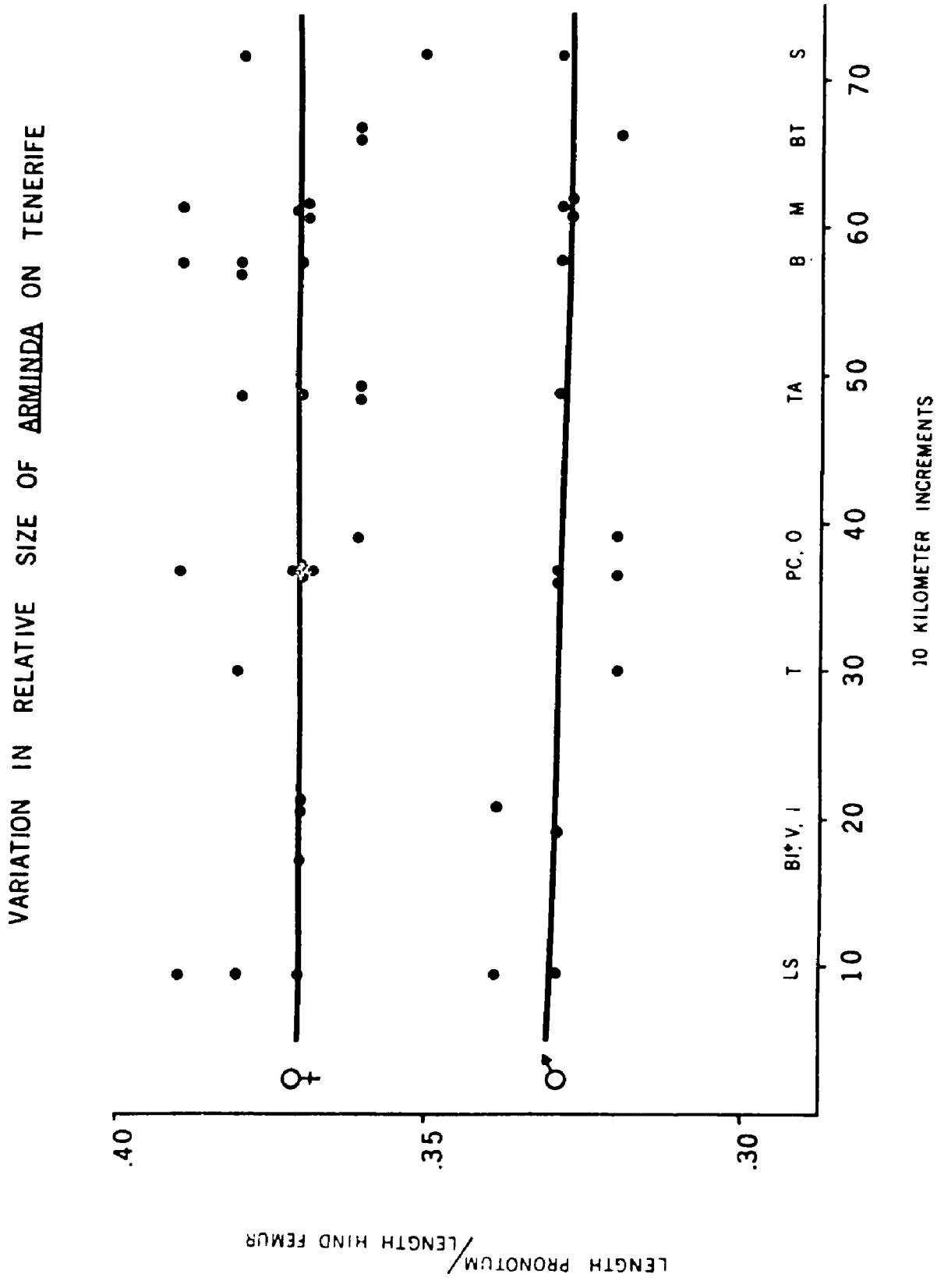
1) The Tenerifean Armindas have a wide distribution, ranging the whole 78 km east to west distance along the north coast of the island (Map 9). One female from the peculiar Barranco del Infierno on the southwest coast of the island suggests a wider distribution on this less populous coast than is indicated by collection data.

2) Specimens from all localities are within the same size range, based on hind femur and pronotum measurements (Fig. 7).

3) The morphology of the dorsal lobe of the aedeagus shows essentially no variation among localities. All specimens studied closely resemble the example from San Andrés, the type locality of A. brunneri and appenhageni (Fig. 6 I). One male from La Vega on the northwest coast of Tenerife is of doubtful status; it is indistinguishable from A. burri from Gran Canaria.

4) Features of the external male genitalia do not vary systematically from locality to locality. For example, the supra-anal plate varies in shape from nearly square to slightly elongate, both in series

FIGURE 7. Regression lines showing variation in relative size of Arminda on Tenerife. Specific localities of collection are arranged in west to east order. Sites except for BI^+ are located on the north coast of the island. LS = Los Silos; BI^+ = Barranco del Infierno; V = La Vega; I = Icod; T = Tigaiga; P = Puerto de la Cruz; O = Orotava; Ta = Tacoronte; B = Bajamar; M = Mercedes; BT = Barranco Tahodio; S = San Andrés.


VARIATION IN RELATIVE SIZE OF ARMINDA ON TENERIFE
LENGTH PRONOTUM/LENGTH HIND FEMUR
.40
.35
.30
♀
♂
LS
BI*V, I
T
PC, O
TA
B
M
BT
S
10
20
30
40
50
60
70
10 KILOMETER INCREMENTS

from a single locality and throughout the range represented. Cerci are straight and slightly longer than the supra-anal plate in all cases observed.

5) Females from single localities cannot be distinguished from those of other localities. Body shape, coloration, features of the external genitalia and morphometric characters are more variable in this sex than in males. For example, general body shape in females varies from a stocky and robust form to slender, both at a given locality and over the range of localities. Relative body proportions of males, on the other hand, are very constant. Enderlein (1929) used the angulation of the dorsal ovipositor valve to distinguish between the holotypes of A. brunneri and A. appenhageni. His illustration of this valve, supposedly characteristic of appenhageni, resembles a typical lower ovipositor valve of Arminda, rotated 180^{o}, i.e., with ventral side up. This type of structure was not seen in any of the 60 female specimens studied from any locality, including the type locality of A. brunneri and A. appenhageni. It is suggested that the upcurved, toothless lower valve of Enderlein represents an unusually worn structure.

On the basis of study of the material at hand, the ambiguity in the descriptions of Enderlein's female holotypes and the overlap in type localities, I have concluded that Arminda from Tenerife represents one widely dispersed taxon, the females of which are quite variable, both within a single collection area and over the whole extent

of the range, and the males of which are morphologically conservative and constant. Hence, Arminda appenhageni Enderlein 1929 and A. striatifrons Enderlein 1929 are here considered to be synonymns of A. brunneri Krauss 1892.

Although Arminda latifrons Enderlein 1930 is known from Gomera, and A. hierroënsis occurs on Hierro, these taxa could not be procured for study. According to Johnston (1956) both types are housed in the Berlin Museum. However, correspondence with Dr. K. K. Günther of that institution indicated that the types could not be located, either at Berlin or the Polish Academy at Warsaw.

Chopardminda was described in 1941 by Morales Agacino as a subgenus of Arminda. It is an endemic of the island of Gran Canaria, and according to Agacino has been taken only a few times (personal communication). I collected a single female specimen of Chopardminda on a steep broken lava slope under a shrub of Salvia canariensis between San Nicolas and Tazartico at 660 meters. The species was extremely rare in the locality since several hours of searching did not reveal further specimens. A male specimen procured on loan from the British Museum (Natural History) was collected at Tejeda at approximately 1400 meters, on the same island.

Chopardminda differs from Arminda in several striking features. Chopardminda is of large size (total body length: ♀ 25 mm; ♂ 17.2 mm), approached only by A. burri, also of Gran Canaria (Table 5).

Chopardminda has a hirsute and strongly tuberculate integument, with lateral carinae irregular and callous and with a five-lobed apex of the female subgenital plate. The female of Chopardminda is brightly red-pigmented on the inner surface of the hind femurs and ventral abdomen. Arminda, on the other hand, tends to be small in size (Table 5), has a smooth integument, and uncalloused incurved lateral carinae. The subgenital plate of the female of Arminda is angular or with bilobate apex.

Family: Acrididae
Subfamily: Oedipodinae
Genus: Acrotylus
Species on the Canary Islands: Acrotylus insubricus (Scopoli, 1786)
Acrotylus longipes (Charpentier, 1843)
Acrotylus patruelis (Herrich-Schaffer, 1838)

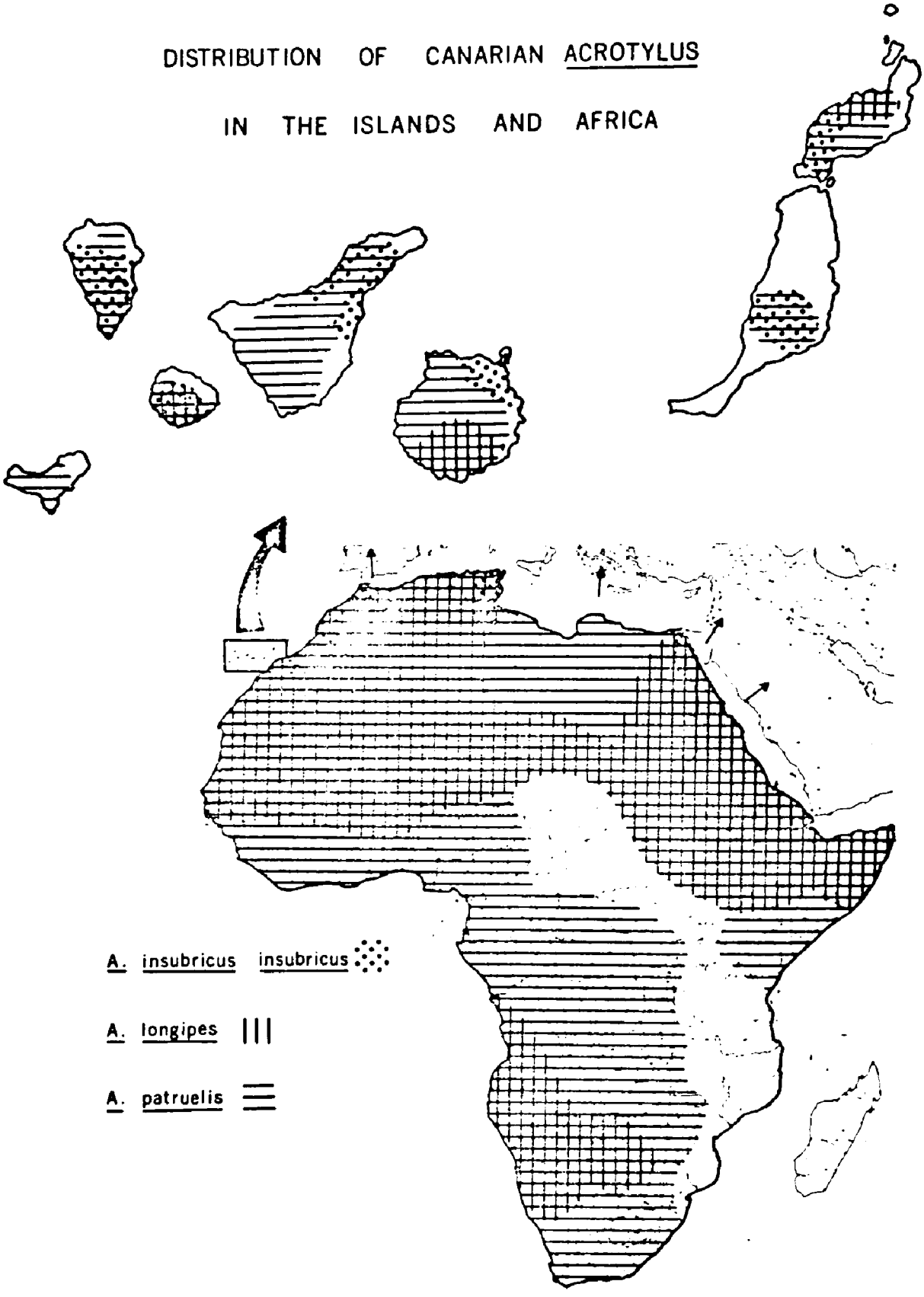
Three species of Acrotylus are known from theCanary Islands, insubricus, longipes, and patruelis. All three have broad distributions in Africa, southern Europe and Asia (Map 10). In 1958, Mařan monographed the species insubricus, distinguishing four subspecies on morphological grounds. The Canarian material appears to belong to the subspecies insubricus insubricus found only in North Africa and southern Europe (Map 10).

A. longipes may easily be distinguished from the other species by the bright yellow wings which lack a darkly pigmented fascia. A. patruelis and insubricus both have red wings with a dark fascia. These latter species may be distinguished from each other by the following

MAP 10. Distribution of Canarian Acrotylus in the Islands and Africa.

DISTRIBUTION OF CANARIAN ACROTYLUS

IN THE ISLANDS AND AFRICA



characters: pronotum rounded at base, body elongate, antennae longer than head and pronotum together in patruelis; pronotum sharply angled at base, body short, antennae shorter than head and pronotum together in insubricus.

Although Acrotylus is mainly an open sand inhabitant in Africa and Eurasia (Chopard, 1943), patruelis was collected in a variety of habitats in the Canaries ranging from the desolate open lava at Fuencaliente, La Palma, at 10 meters, and sand beach at Maspalomas, Gran Canaria, to the grassy meadows of Aguamansa, Tenerife, at 1200 meters. The highest elevation at which this taxon is known is 2000 meters at Los Roques, La Palma, where the species was found on open lava. A. longipes has been collected only below 300 meters and appears to be limited to the littoral semi-desert zone on the Canaries. Adults of longipes were taken in May on Lanzarote, while adults of patruelis were found from January to September on Tenerife.

I did not collect A. insubricus insubricus in the Islands. However, the locality data of Willemse and Bruijning (1949), and Willemse (1950) allow preliminary conclusions concerning the ecology of this species on the Islands. A. insubricus insubricus is reported from sea level to 650 meters on La Palma, Tenerife and Gran Canaria. Most of the localities given in the above sources are coastal, but a few are open, cultivated areas in the semi-desert and forest zones. Specific locality data were not available for Gomera, Fuerteventura and Lanzarote for this species; stipling indicates likely distribution based on knowledge of i. insubricus on other islands (Map 10).

Family: Acrididae
Subfamily: Oedipodinae
Genus: Aiolopus
Species on the Canary Islands: Aiolopus strepens (Latreille, 1804)
Aiolopus thalassinus (Fabricius, 1781)

Aiolopus strepens and A. thalassinus were first reported from the Canary Islands by Brullé in 1840 as Anacridium vittatum and A. laetum, respectively. Finot (1895) placed these species in their correct taxa.

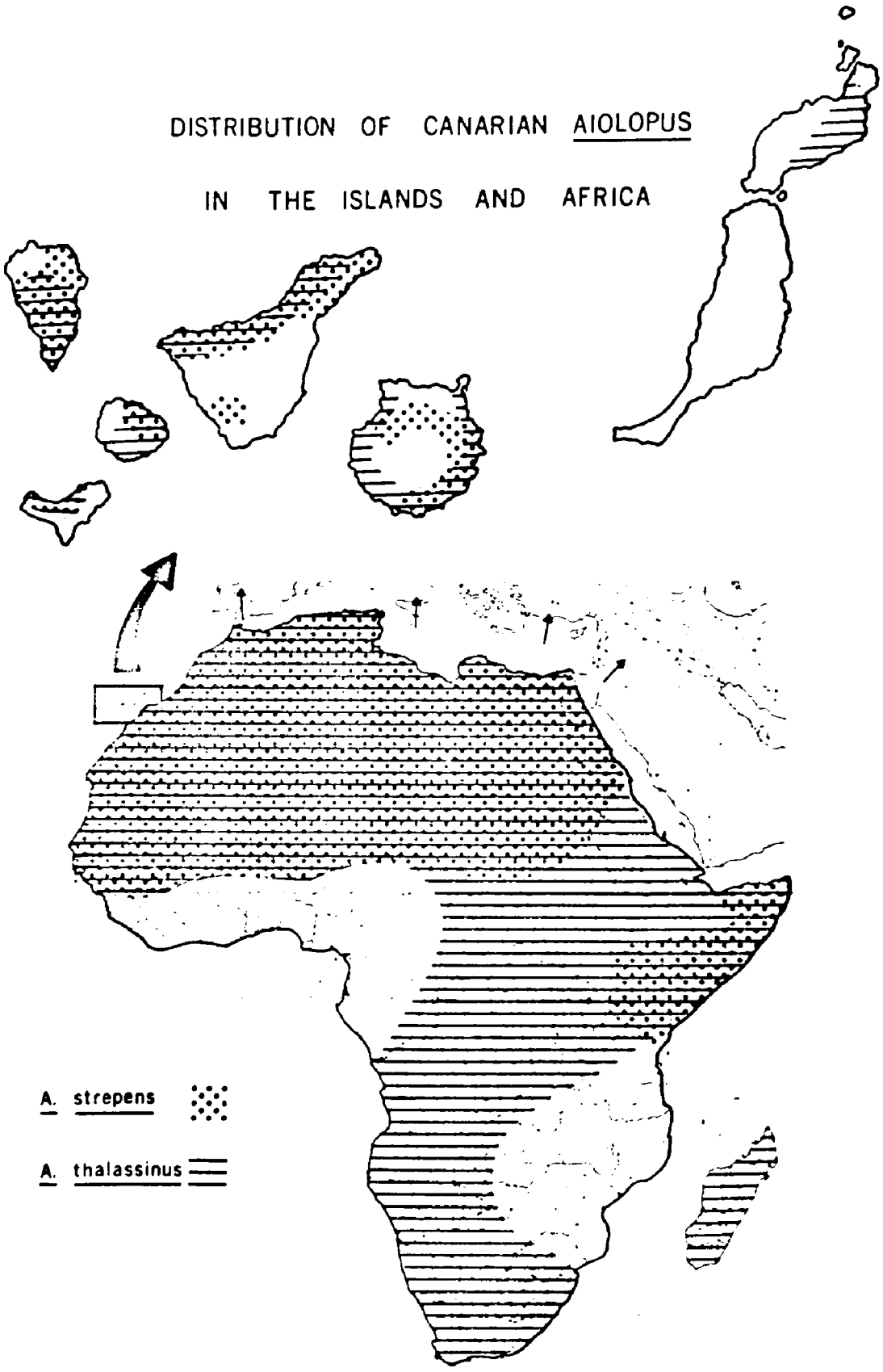
Although Chopard (1951a) reports that these are difficult taxa to distinguish, Canarian material of the two species differs markedly in at least three characters. The elytra of strepens are pigmented in a pantherine pattern from base to tip. This is not true for thalassinus. Pigmentation is usually diffuse in this species and if pantherine, the pattern terminates about one-half way from the base of the elytra. The wings of strepens are always with dark brown pigmentation which extends from the tip of the wing into the vannal area. Usually the hind wings of thalassinus are completely clear, occasionally with pale brown pigmentation in the tip. The hind tibia of both sexes of strepens is bright red along its entire length; in thalassinus the hind tibia is characteristically pale tan, occasionally red in the distal half.

The two species are sympatric over much of their range (Map 11). A. strepens is concentrated in North Africa; thalassinus extends south to the Cape. Often, in the Canaries, I collected the species together, usually in cultivated or in green grassy areas. Occasionally an individual was taken in an open habitat, such as that found at the

MAP 11. Distribution of Canarian Aiolopus in the Islands and Africa.

DISTRIBUTION OF CANARIAN AIOLOPUS

IN THE ISLANDS AND AFRICA



narrow Barranco del Infierno, Tenerife. Hafez and Ibrahim (1962) report that thalassinus is found in humid habitats, often associated with Cynodon dactylon, the common Burmuda Grass. In the Canaries, Aiolopus is found from about 150 meters in the xerophytic zone upward to the pine belt.

MATERIAL STUDIED (UMMZ) A. strepens. LA PALMA: El Time 590 M, 7 ♀, 5 ♂, May; Fuencaliente 600 M, 1 ♀, May; Fuencaliente 400 M, 1 ♀, September; Road to Barlovento, 2 ♀, 2 ♂, September; Road to Roque Faro 1200 M, 1 ♂, May. TENERIFE: Field near Mercedes 700 M, 11 ♀, 15 ♂, January; San Andrés 175 M, 4 ♀, April; Castillas 550 M, 1 ♀, April; Laguneta Alta, 1 ♀, February; Barranco del Infierno, 1 ♀, May; Aguamansa pasture, 8 ♀, 2 ♂, March; Heath above Aguamansa 1320 M, 1 ♀, February; Field above Raices 1300 M, 2 ♀, February. GOMERA: Barranco Ville, 1 ♀, 1 ♂, March; El Cedro 1000 M, 2 ♀, 4 ♂, March; Cumbre Carbonera 630 M, 2 ♀, March. A. thalassinus. TENERIFE: Orotava, 425 M, 14 ♀, 2 ♂, 2 nymphs, October; Orotava 400 M 1 ♀, May; San Andrés 250 M, 3 ♀, 5 ♂, April; Puerto de la Cruz 100 M, 3 ♀, 2 ♂, February; Las Mercedes 700 M; 3 ♂, January. GRAN CANARIA: Agaete 160 M, 1 ♂, June; Taidia 750 M, 1 ♂, June; San Nicolas 50 M, 2 ♀, 1 ♂, 1 nymph, June; Mogan 770 M, 3 ♀, 1 ♂, June. LA PALMA: Fuencaliente 600 M, 1 ♀, September; El Paso 900 M, 1 ♂, May; El Time 590 M, 1 nymph; May. GOMERA: Cumbre Carbonera 630 M, 1 ♀, 4 ♂, March; Valle Gran Rey 600 M, 3 ♀, 6 ♂, March.

Family: Acrididae
Subfamily: Oedipodinae
Genus: Locusta
Species on the Canary Islands: Locusta migratoria (Linnaeus 1758)

Locusta migratoria has a wide non-insular distribution in Europe, Asia, Africa and Australia. Uvarov (1966) recognized at least eight subspecies of migratoria based on morphometric grounds. It is likely that Canarian material belongs to Reiche and Fairmairès m. migratoriodes (1850).

The Canarian forms have never been known to swarm naturally, and tend to be small as compared with mainland m. migratoriodes (Uvarov, op. cit.). All of the specimens seen from the Canaries were of the solitaria phase, characterized by a raised pronotal crest and uniform green coloration. Apparently, unlike the gregaria phase, this phase is adapted to the immediate environment (Faure, 1932; Hertz and Imms, 1937; Ergene, 1952). According to Roonwal (1952), the number of hopper instars as well as number of antennal segments is increased in the solitaria phase as compared with the gregaria phase.

I collected this species in localities between 200 and 650 meters on the islands of Gran Canaria, Tenerife, Gomera and La Palma (Map 12), the four central islands of the archipelago. It is usually found in green, shrubby areas, occasionally in disturbed or cultivated areas (Table 6). Locusta often occurred in association with Scintharista notabilis, which shares the same general insular distribution (Map 15). Interestingly, the species is not found on the two islands closest to

MAP 12. Distribution of Locusta migratoria in the Canary Islands and Africa.

DISTRIBUTION OF LOCUSTA MIGRATORIA IN

THE CANARY ISLANDS AND AFRICA

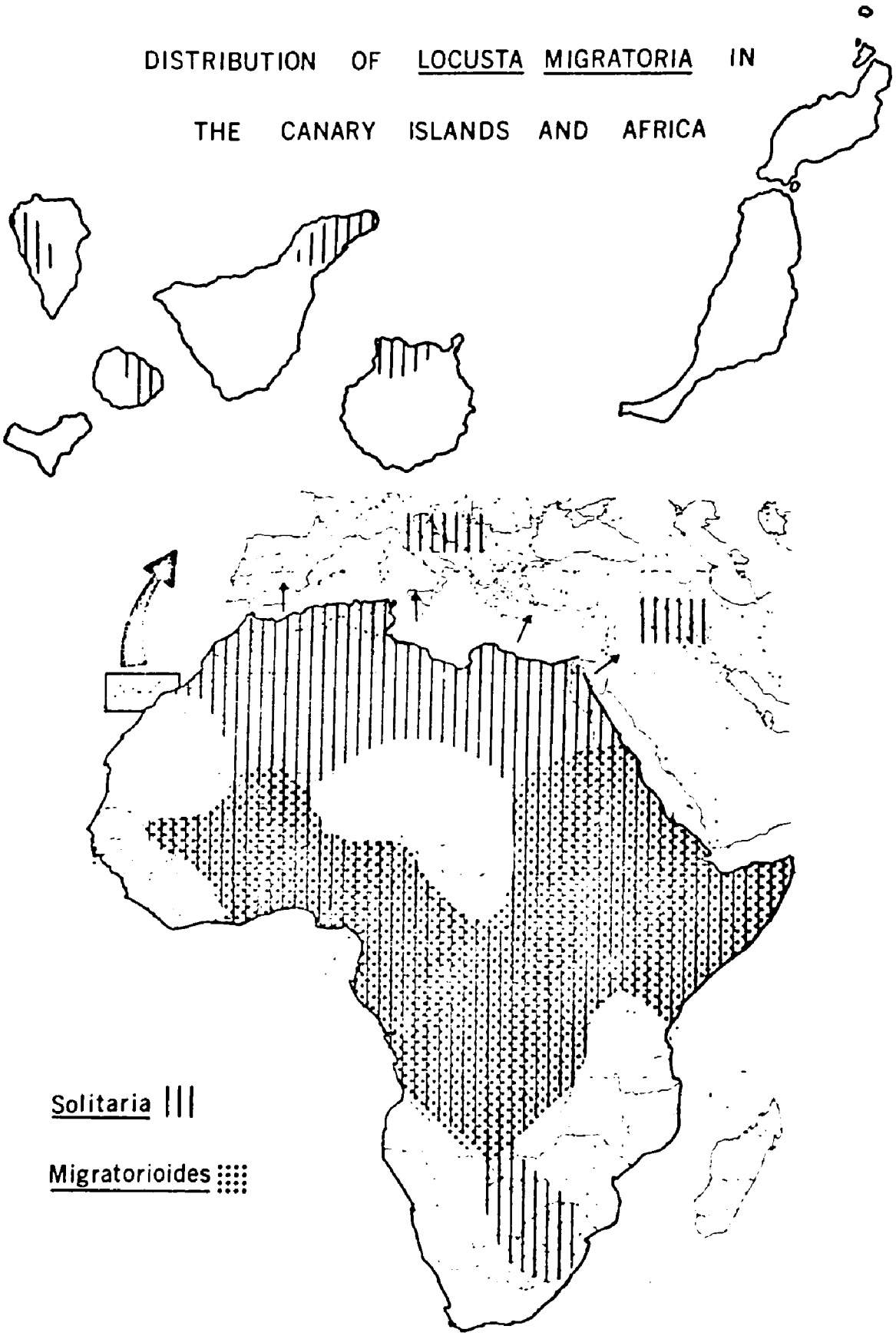


TABLE 6. Vegetation at collecting sites of Locusta migratoria on Gomera and La Palma.

Plant species	Life form	Family	Barranco Ville 630M Gomera	Lomo Caballo 580M La Palma
Euphorbia bertheloti	N	Eupho.	1	
Kleinia neriifolia	N	Compo.	+	
Plocama pendula	N	Rubia.	1	
Opuntia tuna	SS	Cacta.		+
Aeonium viscatum	Ch	Crass.	+	
Lavandula abrotenoides	Ch	Labia.	1	
Micromeria sp.	Ch	Labia.	+	
Phagnalon rupestre	Ch	Compo.		+
Picridium ligulatum	Ch	Compo.	+	
Psoralea bituminosa	Ch	Legum.	+	+
Andropogon hirtus	H	Grami.	1	1
Cynara cardunculus	H	Compo.		2
Notholaena vellea	H	Pteri.	+	
Pennisetum cenchroides	H	Grami.	+	
Sanguisorba verrucosa	H	Rosac.		+
Asphodelus sp.	G	Lilia.	1	1
Bidens pilosa	T2	Compo.	+	
Echium plantagineum	T2	Borag.	1	1
Galactites tomentosa	T2	Compo.	+	+
Anagallis arvensis	Th	Primu.	+	
Avena barbata	Th	Grami.	+	1
Bromus rubens	Th	Grami.		2
Calendula arvensis	Th	Compo.		2

TABLE 6. (Continued)

Plant species	Life form	Family	Barranco Ville 630M Gomera	Lomo Caballo 580M La Palma
Erodium chium	Th	Geran.	+	
Evax pygmaea	Th	Compo.	+	
Pallensis spinosa	Th	Compo.		1
Silene gallica	Th	Caryo.	1	+
Trifolium arvense	Th	Legum.		1
Trifolium glomeratum	Th	Legum.	+	1
Vulpia sp.	Th	Grami.	+	
Periploca laevigata	Li	Ascle.	+	

Africa, possibly because the shrubby, green habitat is absent on these desert-like islands. Chopard (1938) considered this species as a low elevation form on the Island of Madeira.

MATERIAL STUDIED (UMMZ) GOMERA: Cumbre Carbonera 630 M, 6 ♀, 3 ♂, 2 nymphs, March; Barranco Ville 250 M, 1 ♀, 1 ♂, March. TENERIFE: Castillas 550 M, 2 ♀, April; San Andrés 250 M, 2 ♂, April. LA PALMA: El Time 590 M, 1 ♀, May; Lomo Caballo 580 M, 6 ♂, 3 nymphs, May. GRAN CANARIA: East of Guia 200 M, 2 ♂, June.

Family: Acrididae
Subfamily: Oedipodinae
Genus: Oedaleus
Species on the Canary Islands: Oedaleus decorus (Germar, 1826)
Oedaleus senegalensis (Krauss, 1877)

Oedaleus decorus was first reported from Tenerife in 1915 by I. Bolivar under the name Oedaleus nigrofasciatus, a species now recognized as mainly African (Johnston, 1956, 1968). Previous to I. Bolivar's report, Burr (1911) referred to a "... Canarian representative of O. nigrofasciatus" ... between 2000-3000 meters in ..." the viney cultivated"... areas of Tenerife and also near the bottom of the heath zone near Agua Garcia of the same island. Although he identified this species as O. senegalensis, it is likely that his material represented O. decorus since senegalensis has not been recorded before or since from any island other than La Palma.

I have not seen specimens of O. decorus from the Canaries,

and, except for information gleaned from the literature, I have little ecological data on the species. Burr (1912) reported that decorus is rare, but present at low elevations on the Atlantic Islands (including Madeira); Chopard (1938b) indicated that in Madeira, decorus is abundant only in the high montane range above 1500 meters. However, in another paper on the desert fauna of Africa (1938a), Chopard classified decorus with the oasis habitat rather than the montane.

O. decorus has a wide non-insular distribution in North Africa, Somaliland, Europe and Asia (Johnston, 1956, 1968) (Map 13). Chopard (1951 a) reports that decorus is the only known Oedaleus in France.

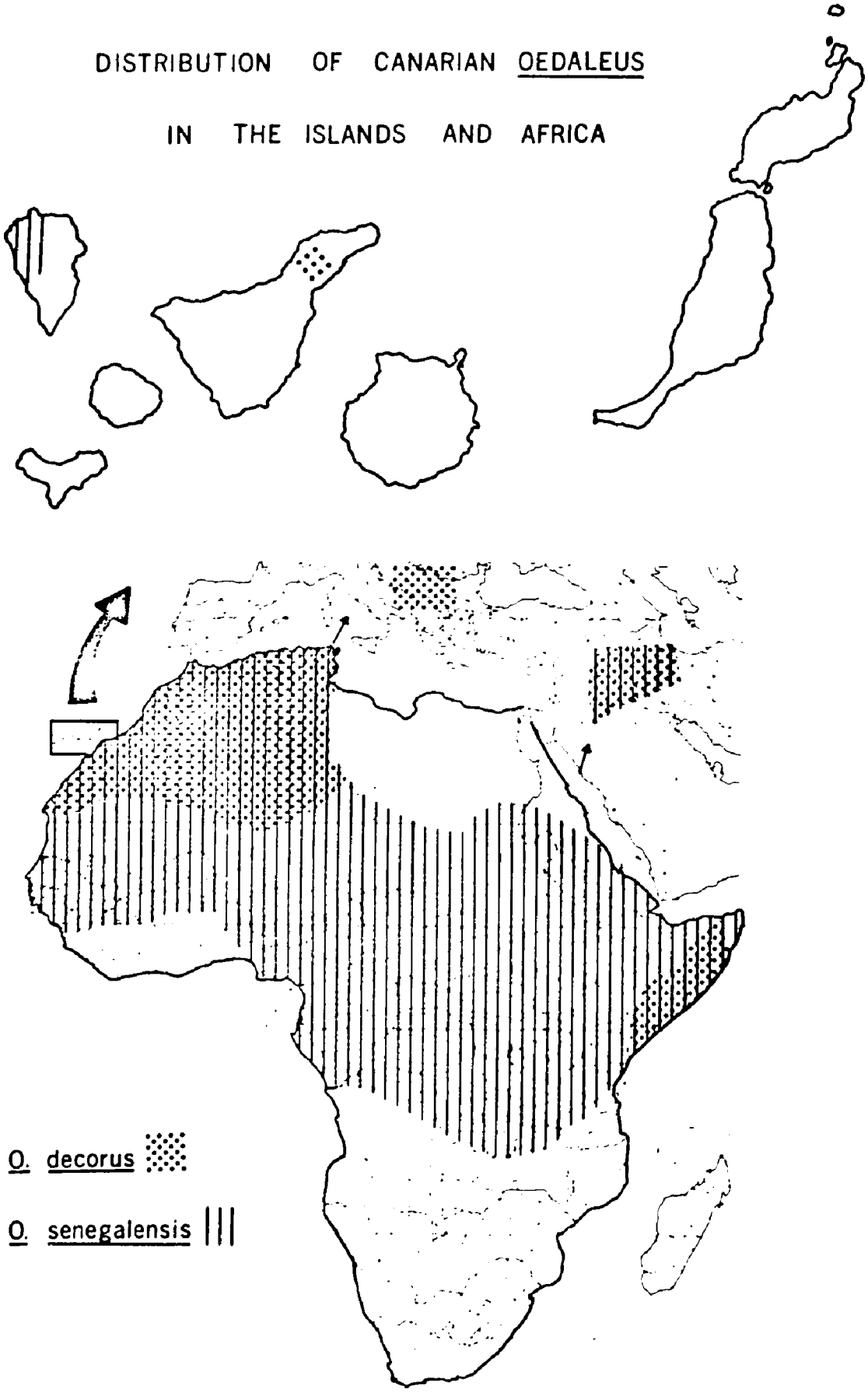
Oedaleus senegalensis was first reported from the Canary Islands by Krauss (1892). In this paper, Krauss made no comments about the species except that it occurred on the island of La Palma. It has been collected on this island many times since, most recently reported by Chopard, 1954. The species is also known from the Cape Verde Islands (Johnston, 1956), and exhibits a non-insular distribution throughout much of Africa and southwestern Asia (Map 13).

I collected senegalensis at El Time, La Palma, at 590 meters in an open field. Joyce (1952) reports that in East Central Sudan, it is common in short grass and open areas. O. senegalensis is further reported by Joyce to be occasionally gregarious. In Sudan, he has observed dense swarms of this species "marching" in bands, both alone and mixed with Schistocerca gregaria.

MAP 13. Distribution of Canarian Oedaleus in the Islands and Africa.

DISTRIBUTION OF CANARIAN OEDALEUS

IN THE ISLANDS AND AFRICA



Family: Acrididae
Subfamily: Oedipodinae
Genus: Oedipoda
Species on the Canary Islands: Oedipoda caerulescens (Linnaeus, 1758)
Oedipoda canariensis Krauss, 1892
Oedipoda fuscocincta Lucas, 1849

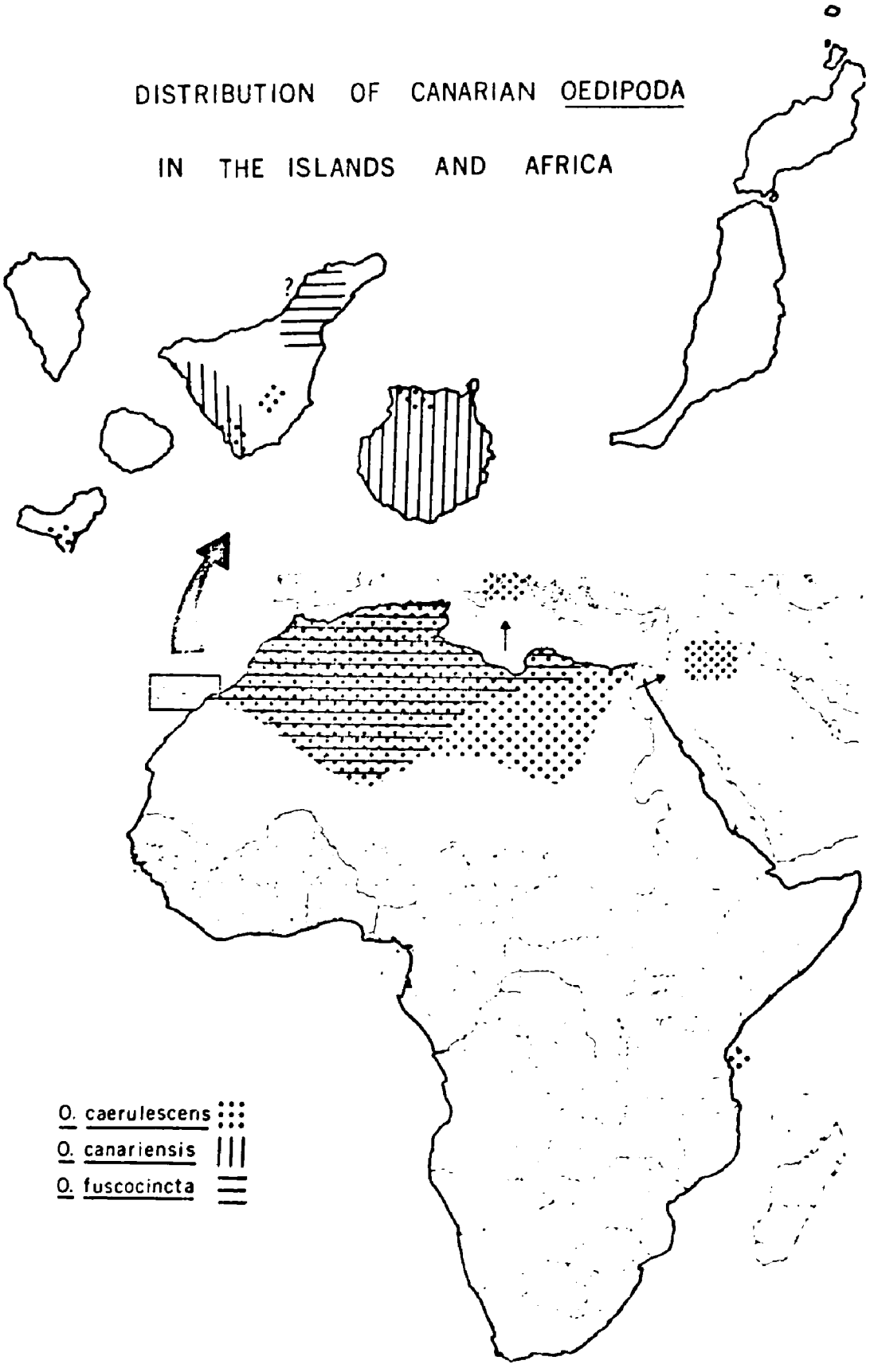
Oedipoda fuscocincta was first reported from the Canary Islands by Bormans (1885). No material of this species was available to me for study, and the only reference to a specific insular distribution was made by Chopard (1954) in an identification which he questioned while classifying specimens taken by Lindberg and Frey on Tenerife.

O. canariensis is endemic to the Canary Islands and the Azores. Krauss considered his new species a close relative of O. caerulescens. He distinguished between the two on the basis of pronounced rugosity of the head and pronotum and very broad pigmentation pattern on the otherwise hyaline wing of canariensis.

Two morphologically distinctive, but closely related forms are indeed found in my small collection of Oedipoda from the Canary Islands. These correspond to the descriptions of caerulescens and canariensis. Since their ranges are occasionally sympatric on the Islands, I have questioned the possibility that this series represents not two, but one species on the Canaries with rather variable morphology. For purposes of species enumeration and because I lacked a large enough series for morphometric analysis, I found it necessary to map both (Map 14).

Oedipoda is absent on Lanzarote and Fuerteventura, has a

MAP 14. Distribution of Canarian Oedipoda in the Islands and Africa.


DISTRIBUTION OF CANARIAN OEDIPODA
IN THE ISLANDS AND AFRICA
?
O. caerulescens
O. canariensis
O. fuscocincta

wide distribution on Gran Canaria, and is poorly represented on the more western islands. From the point of view of possible derivation of the canariensis form, it is interesting that those specimens resembling the continental caerulescens have the broadest range on the Canaries. I collected material of caerulescens at the Barranco del Infierno, 240 meters, Chio at 810 meters, Vilaflor at 1400 meters on Tenerife, and at one locality on Gran Canaria, Guia 200 meters. O. canariensis was collected with caerulescens at Chio, Tenerife. It is common on Gran Canaria where it is found from near sea level at Barranco Agaete (160 meters) to the Roque Nublo at 1700 meters.

Family: Acrididae
Subfamily: Oedipodinae
Genus: Scintharista
Species on the Canary Islands: Scintharista notabilis notabilis (Walker, 1870)

The genus Scintharista has been reported to occur in the Canary Islands, Spain, North Africa and southern Asia. Six species are known from Africa; one, notabilis, ranges from the Canary Islands east into northwestern India, and north into the Iberian Peninsula. Within this area, distribution is often discontinuous, coinciding with systems of old eroded mountains fringing desert environments (Uvarov, 1941).

Uvarov, in his revisionary study (op. cit.), recognized seven subspecies of notabilis, of which only the nominate form is found in the Canary Islands. N. notabilis is also known from North Africa and

southern Spain. Johnston (1968) added Niger Colony in West Africa to this range (Map 15).

I collected this subspecies on three of the Canary Islands, Tenerife, Gomera and La Palma. Gardner (1960) also has a record for notabilis notabilis from Guia, Gran Canaria. In all cases, the elevation of collected areas was 200 meters and above; the highest was at Vilaflor, Tenerife, at 1400 meters. The form was always collected amid the sparse vegetation of barren lava beds. This observation is consistent with Uvarov's note (op. cit.) that the taxon tends to occur along barren, rocky slopes.

MATERIAL STUDIED (UMMZ): GOMERA: Barranco Ville 250 M, 8♀, 1♂, March. TENERIFE: San Andrés 250 M, 3♀, 2♂, April; Vilaflor 1400 M, 2♀, 2♂, August. LA PALMA: La Caldera 500 M, 2♀, 1♂, September.

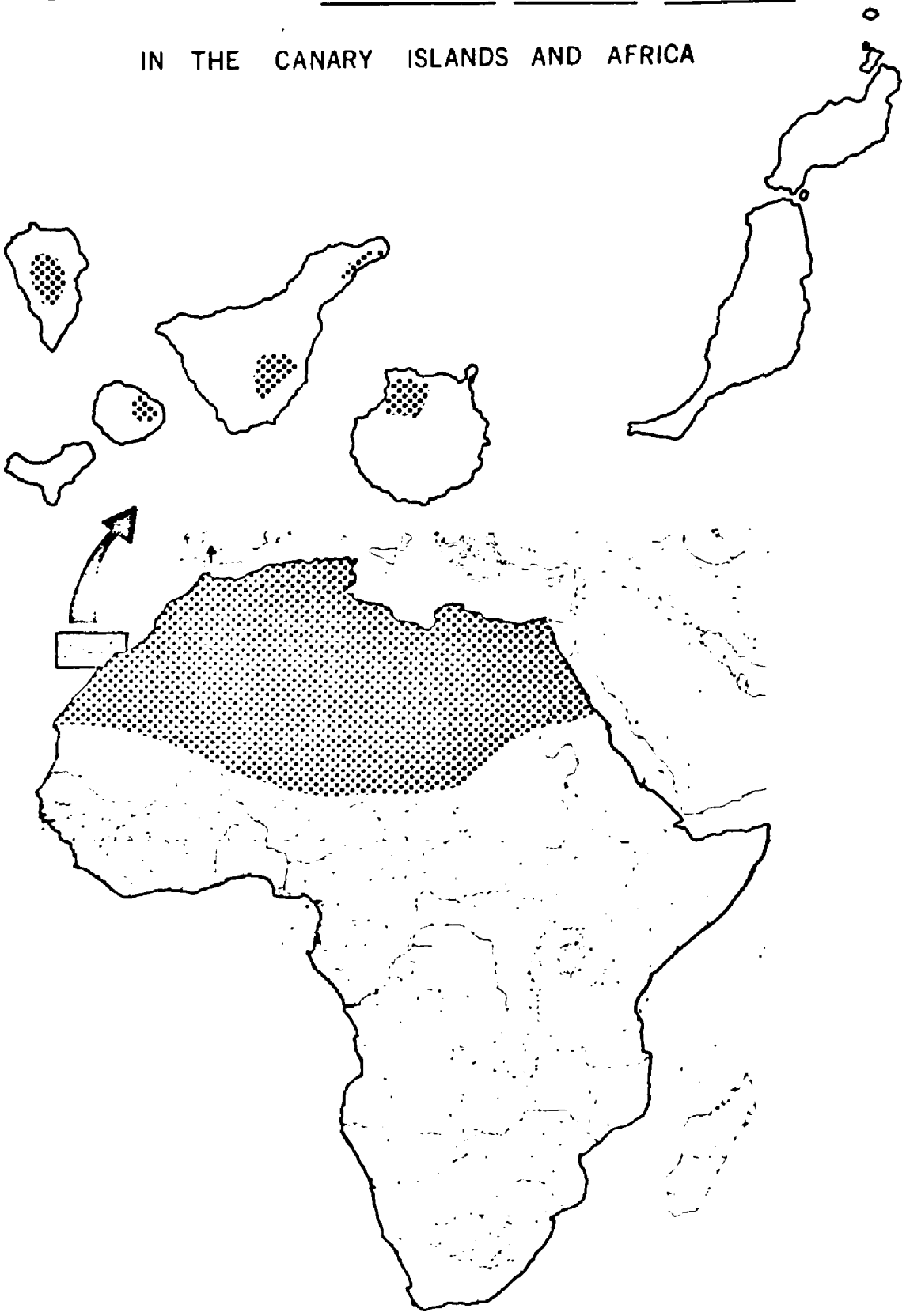
Family: Acrididae
Subfamily: Oedipodinae
Genus: Sphingonotus
Species on the Canary Islands:
Spingonotus caerulans (Linnaeus, 1767)
Sphingonotus canariensis (Saussure, 1884)
Sphingonotus freyi Uvarov, 1948
Sphingonotus lucasii Saussure, 1888
Sphingonotus rubescens (Walker, 1870)
Sphingonotus savignyi Saussure, 1884
Sphingonotus willemsei Mistshenko, 1937

Mistshenko (1936, 1937a), in his revision of the genus Sphingonotus, based recognition of 19 species groups on morphological characteristics, such as coloration of the caudal legs and wings, and

MAP 15. Distribution of Scintharista notabilis notabilis in the Canary Islands and Africa.

DISTRIBUTION OF SCINTHARISTA NOTABILIS NOTABILIS

IN THE CANARY ISLANDS AND AFRICA



rugosity of the pronotum. Neither Uvarov (1948), nor I, working with Canarian material, have found these groups useful in the recognition of new species, or in reflecting the likely course of evolution within groups. As with most Oedipodine genera, this large and nearly cosmopolitan genus is in need of critical revisionary analysis which uses cytogenetic and behavioral information in addition to morphology as characters.

Five of the seven species of Sphingonotus which have been reported from the Canary Islands, have wide distributions in Africa and Eurasia (Map 16). The remaining two species are endemic,[6] freyi on Gran Canaria and willemsei occurring on Tenerife. Within a given species, no morphological differentiation is apparent on or between islands. For this reason, I believe that the non-endemic species reached the Canaries as well differentiated taxa.

Sphingonotus rubescens and S. caerulans are somewhat of a systematic problem on the Canary Islands. Apparently, they are frequently mistaken, one for the other. Often, specimens of the two "species" identified by the same investigator as different, cannot be distinguished except by locality. The literature prior to 1954, as well as my own collections point to a wide distribution of S. caerulans on all of the Islands. Material borrowed from Madrid and Geneva and identified as S. rubescens is from Tenerife only. However, Chopard's

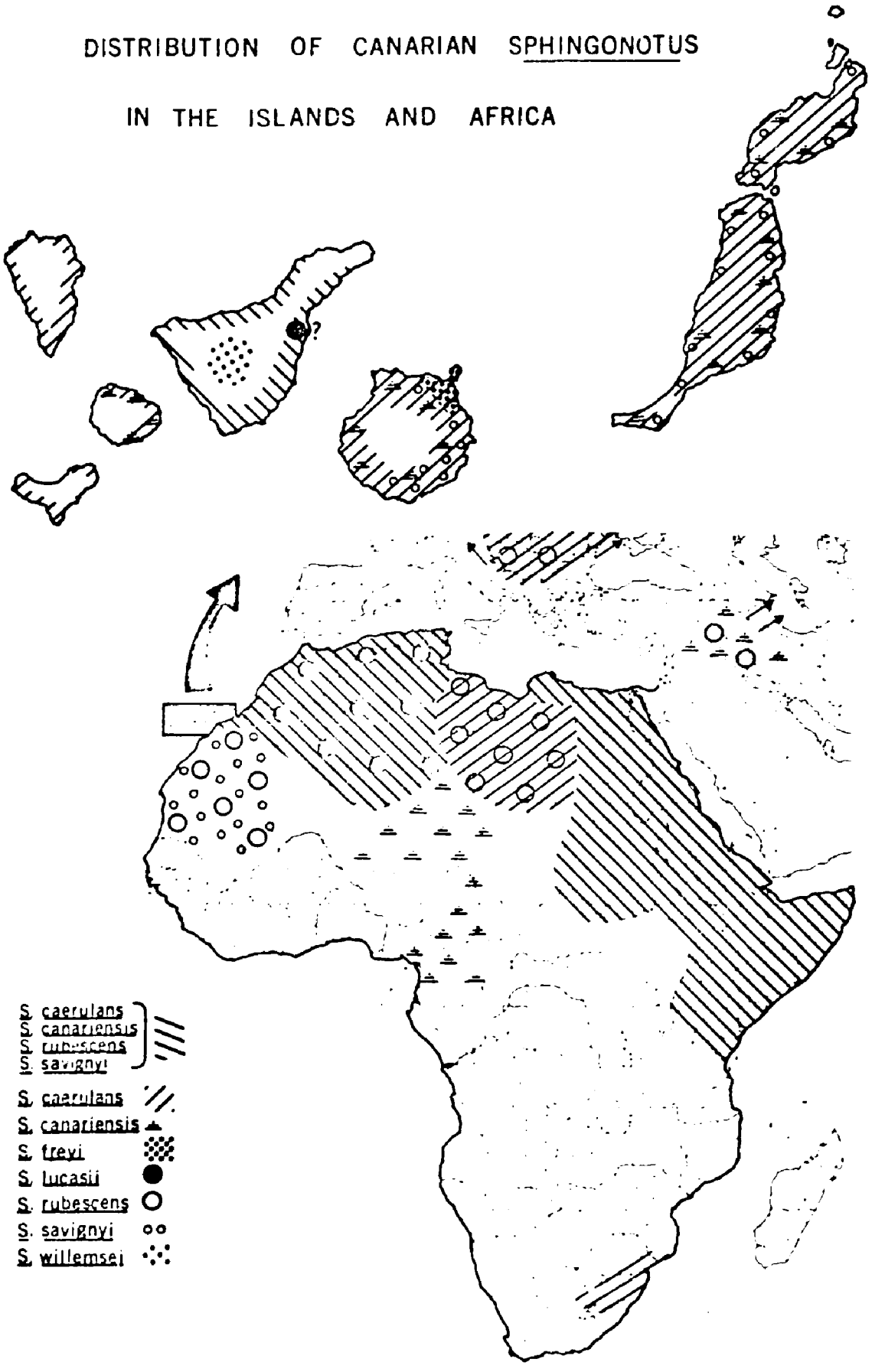
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[6] S. teydei and S. willemsei from Tenerife cannot be distinguished on morphological grounds and are grouped as S. willemsei (Map 16).

MAP 16. Distribution of Canarian Sphingonotus in the Islands and Africa.

DISTRIBUTION OF CANARIAN SPHINGONOTUS

IN THE ISLANDS AND AFRICA



1954 paper classifying Orthoptera collected by M. H. Lindberg on the islands reports S. rubescens as occurring on all of the islands; and although, essentially all other known species in the genus found in the Islands are enumerated in his work, S. caerulans is rather obviously missing. Since distinctions between these two species will probably be based on other than morphological criteria, I leave the question as it stands, and have mapped distributions according to the prevailing opinion.

In 1937 b Mistshenko described S. willemsei on the basis of nine specimens from Montaña Blanca, Cañadas region, Tenerife, sent to him by Uvarov. The female type and male allotype were deposited in the Zoological Institute, USSR Academy of Sciences, Leningrad, and paratypes were sent to the British Museum (Natural History). In 1948, Uvarov described S. teydei, based on a small collection from the same area; the male type and four paratypes are in the Helsinki Zoological Museum, and two paratypes are in the British Museum (Natural History). I have concluded on the basis of the observations recorded below that teydei is a synonym of willemsei.

Paratypes of willemsei were obtained from the British Museum, a series of specimens identified as teydei/willemsei by Morales Agacino was borrowed from his collection, and I personally collected additional material from the area where both were supposed to occur. The differences between the two noted by Uvarov were tabulated (Table 7), and the 39 specimens assembled for study were examined in detail,

TABLE 7. Comparison of Sphingonotus willemsei and S. teydei from the literature.

Character	♂ willemsei	♂ teydei
Size pronotum	3.4 - 3.5 mm	4.5 mm
Elytra coloration	Scattered dark spots in the apical half	Scattered dark spots in the apical half; with two dark irregular fasciae
Hind femur coloration	Basal half inner surface blue-black; with two pale fasciae	Basal half inner surface blackish; with a black preapical fascia
Hind tibia coloration	Dark blue	Dirty yellow (discolored ?)
General body size	Medium	Medium
Presence of hairs	Short white hairs	Soft, white hairs
Head position and punctation	Head ± raised above pronotum. Finely punctured	Head well prominent above pronotum. Scarcely punctate
Fastigium of the vertex	Strongly sloping	Weakly sloping
Transverse sulci of the pronotum	Distinct	Very distinct
Length of elytra	5.4 X width	5.0 X width
Supra-anal plate	No mention	With two sclerotized triangular lobes; crenulate
Subgenital plate	No mention	Apically truncate

both with respect to those characters and in a search for other distinctions. Although Uvarov stressed the characteristics of the male subgenital and supra-anal plates as distinctive of teydei, they proved to be indistinguishable from those of paratypes of willemsei, and no differences were found among the specimens I examined. Nothing in the body dimensions (Figs. 8, 9), pigmentation of the elytra and hind femur, shape and sculpturing of the pronotum, structure of the ovipositor valves, or coloration of the hind tibia is indicative of specific difference.

The Cañadas of Tenerife, from which both species were described, is a large, uniform pumice field formed by the recent eruption of the Pico de Teide in the extensive ancient crater of the island. It is a true subalpine desert, with a unique and very uniform flora. In August, when my own collections were made, S. willemsei occurs throughout the Cañadas; most of the other collections seen in this study were taken in September. On ecological and evolutionary grounds it seems highly improbable that two closely related members of the same genus could be sympatric in this sharply delimited, restrictive and homogeneous environment.

With the exception of willemsei, which is endemic to the subalpine desert of Tenerife, 2100 meters and above, all members of the genus Sphingonotus are found in the littoral and semi-desert zones, mainly below 300 meters.

S. freyi, an endemic of Gran Canaria, has been collected at

FIGURE 8. Relationship between body length and hind femur in length in male Sphingonotus willemsei (squares) and male S. teydei (circles).

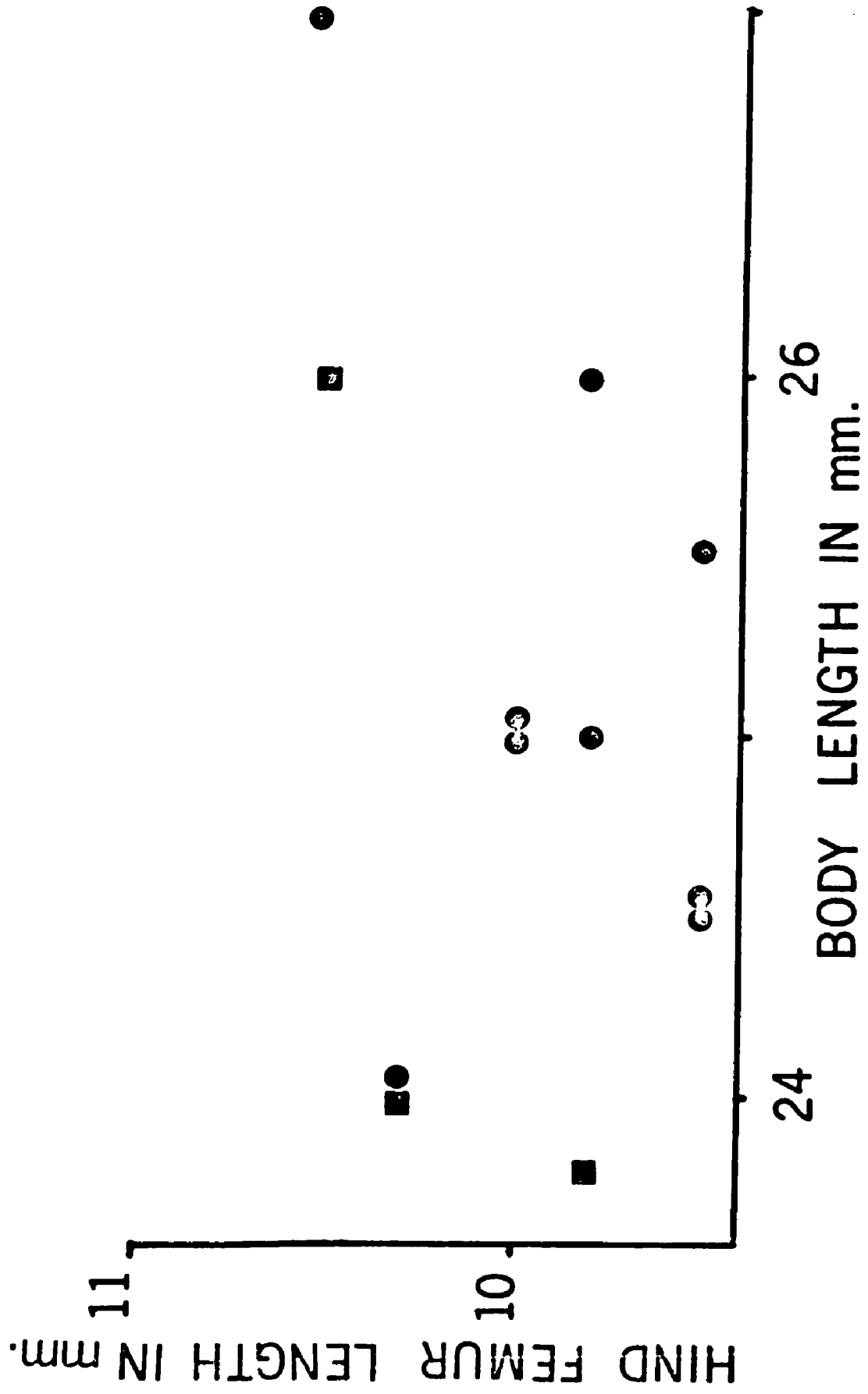
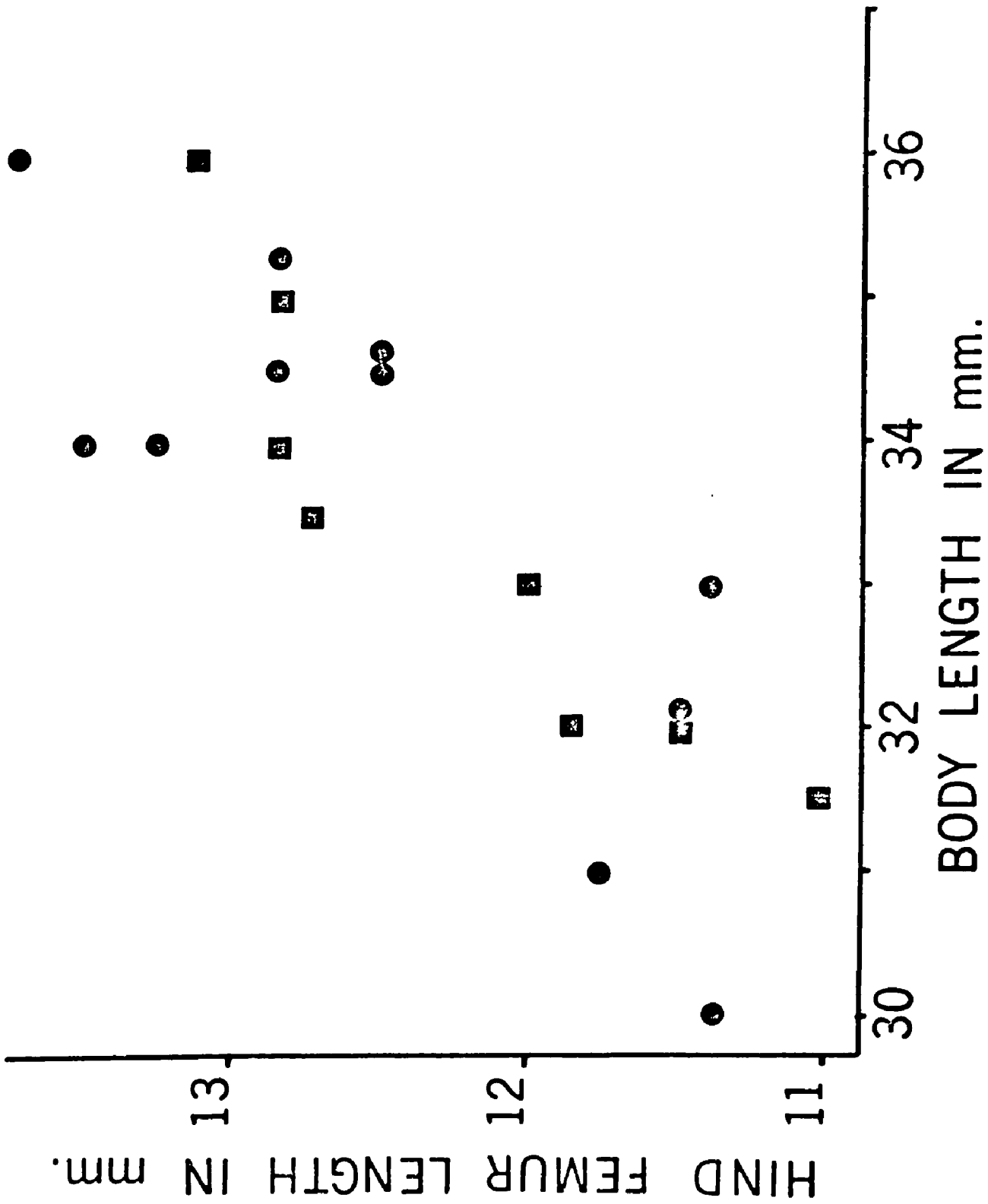

HIND FEMUR LENGTH IN mm.
11
10
24
26
BODY LENGTH IN mm.

FIGURE 9. Relationship between body length and hind femur length in female Sphingonotus willemsei (squares) and female S. teydei (circles).


HIND FEMUR LENGTH IN mm.
11
12
13
30
32
34
36
BODY LENGTH IN mm.

sea level in the outskirts of Las Palmas and Puerto de la Luz.

S. canariensis is often found in open sandy areas and pumice fields below 300 meters.

The three localities for which I have material corresponding to the description of S. rubescens are in the beach and semi-desert zones, Guimar at 300 meters, El Medano at sea level, and Puerto de la Cruz on Tenerife.

S. caerulans is occasionally found above 300 meters on open pumice such as in the Barranco de Masca, 500 meters on Tenerife and at Fuencaliente, 400 meters, on the island of La Palma. In general, however, it is distributed in the semi-desert zone below 300 meters on the Islands.

I have not seen material of S. lucasii from the Canary Islands.

Family: Acrididae
Subfamily: Oedipodinae
Genus: Wernerella
Species on the Canary Islands: Wernerella aspera (Brullé, 1840)
Wernerella pachecoi (Bolivar, 1908)
Wernerella picteti (Krauss, 1892)
Wernerella sublaevis (Bolivar, 1908)
Wernerella sp.

Wernerella is a strictly African genus, with reported localities in disjunct regions on the continent and on islands on the east and west coasts (Johnston, 1956; 1968). W. insularis is found in the eastern-most part of the range of the genus in Socotra (Uvarov and Popov, 1957) and basutensis is endemic to the southernmost part, Basutoland (Dirsh, 1956). The two other species on continental Africa, aspera

and pachecoi, occur in the north. Both of these North African species are found on the Canary Islands, as are three endemic species, picteti, sublaevis and W. sp.

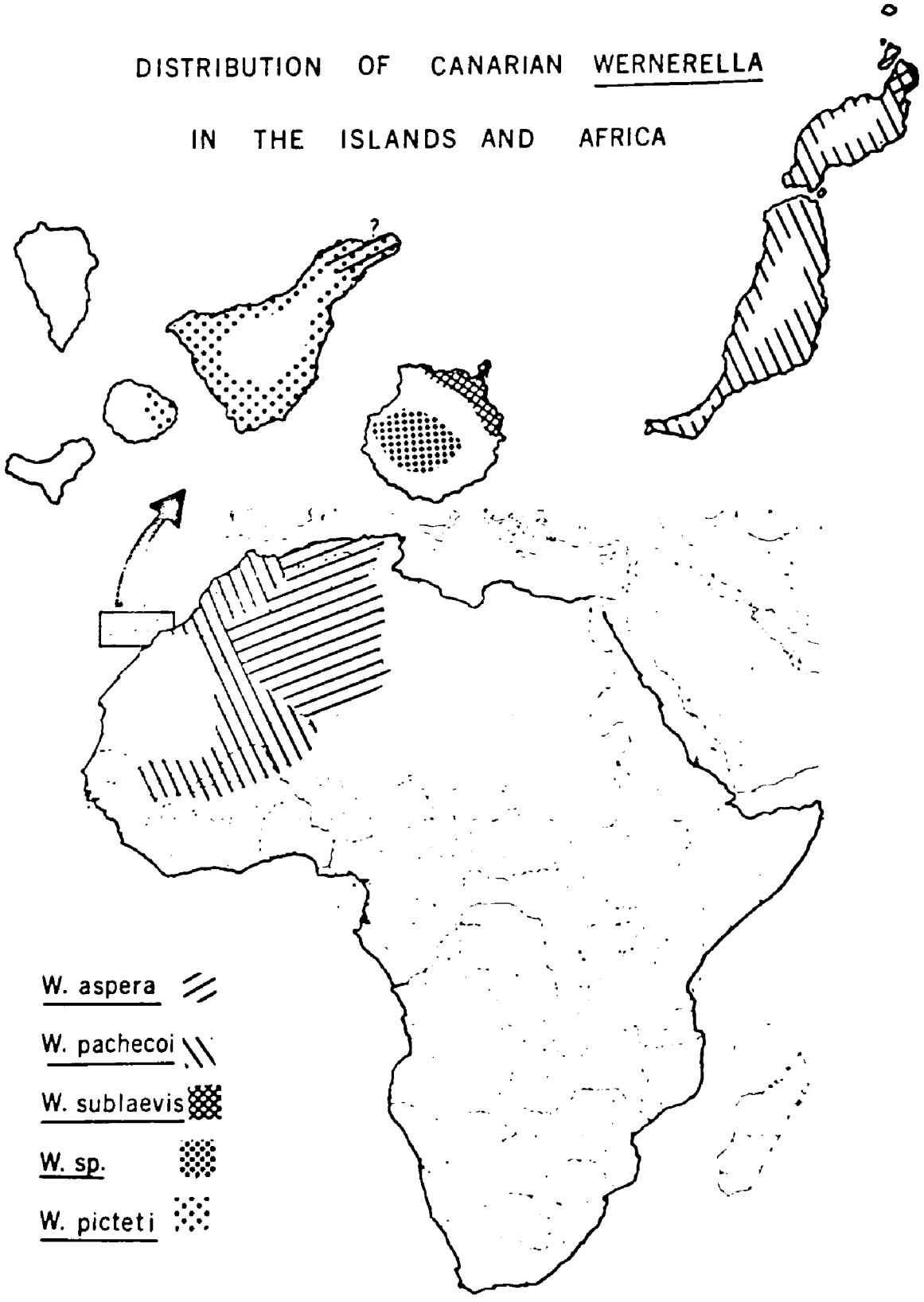
Wernerella aspera was described (Brullé, 1840) from the Canary Islands. No data were given for the types, nor are their whereabouts known (Johnston, 1956, 1968). In the description, Brullé noted the similarity between this species and Sphingonotus caerulans in body shape and coloration. Krauss (1892) extended the distribution of W. aspera to Egypt, and also noted records for this species on Lanzarote and Graciosa (Map 17).

Although no aspera material was available to me, the repeated reference in the literature to similarity with Sphingonotus, suggests that it is quite different from other Wernerellas on the Canaries. In fact, Chopard (1954) relegated specimens collected by Lindberg and Frey on Tenerife to the status Sphingonotus asper. Johnston (1968) lists W. aspera and S. asper as synonyms.

W. pachecoi was described in 1908 by I. Bolivar as Fortunata pachecoi. Although the type material was from Lanzarote, he noted the non-insular distribution in Morocco. Since that time, pachecoi has been collected widely on Fuerteventura and Lanzarote at elevations below 300 meters, and has been reported from Mali in Africa. It is found on open pumice and sparsely vegetated areas on the eastern islands.

I. Bolivar (1908) described W. sublaevis in the same paper

MAP 17. Distribution of Canarian Wernerella in the Islands and Africa.


DISTRIBUTION OF CANARIAN WERNERELLA
IN THE ISLANDS AND AFRICA
?
W. aspera
W. pachecoi
W. sublaevis
W. sp.
W. picteti

with pachecoi. It is endemic to Gran Canaria, is found below 300 meters on sandy soil, and is usually collected along beaches in the littoral zone.

Krauss named picteti in 1892. He gave no specific locality for the species, although other authors have noted localities from Tenerife (Chopard, 1954; Willemse, 1936). I have taken picteti on Tenerife and Gomera. W. picteti is found from sea level to 975 meters; adults may be collected from April to September.

Material received on loan identified as W. picteti from Gran Canaria all represents a new species, a closely related, but distinctive form. W. sp. may be found from the Roque Nublo region of Gran Canaria (2000 meters) to the open pumice fields of San Nicolas at 150 meters on the western coast of the island (Map 17).

The distribution of Wernerella on the Canary Islands is a rather simple one. W. pachecoi is found on the easternmost islands and picteti has the westernmost distribution on Tenerife and Gomera. W. sublaevis and W. sp. are endemic to the centrally located Gran Canaria. Although both sublaevis and W. sp. are found on the same island, their local distributions are allopatric; sublaevis is a sandy beach dweller, while W. sp. tends to be an upland species.

A variety of morphological features of these species was studied in an effort to reflect the possible course of evolution in the group on the Islands. Those characters which are conservative on the species level are enumerated and compared in Tables 8 and 9.

TABLE 8. Classification of characters in Canary Island Wernerella.

Character	pachecoi	sublaevis	new species	picteti
Separation of the carinae of the fastigium of the vertex	far-separated	far-separated	approximate	approximate
Frontal ocellus	large; filling intra-carinal region	large; filling intra-carinal region	small; filling ½-2/3 intra-carinal region	small; filling ½-2/3 intra-carinal region
Body length-male	14.8 ± 1.2 mm	14.6 ± 0.4 mm	15.9 ± 1.4 mm	13.2 ± 1.0 mm
Hairiness of thorax	+ (slightly)	+++ (decided)	+ (slightly)	+ (slightly)
Prozonal ridges lateral to median carina	parallel	parallel	incurved posteriorly	cup-shaped
Pronotal sculpturing	rugose	smooth-punctate	smooth-punctate	rugulose
Mesozonal sculpturing lateral to median carina	incomplete; posterior sides raised	incomplete; posterior sides feebly raised	discontinuous; not raised	fused; forming a feebly depressed obovate area
Hind wing	banded	banded	not banded	not banded
Pigment in first elytra band	continuous	continuous	broken	broken

TABLE 8. (Continued)

Angulation terminus male supra-anal plate	obtuse	acute	obtuse	obtuse
Valves of the cingulum in lateral view	broad, caudal margin straight	broad, caudal margin straight	narrow, caudal margin concave	narrow, caudal margin concave
Apical valve of aedeagus	narrow	narrow	broadened towards base	broadened towards base
Angulation distal end ventral aedeagal valve	120^{o}-130^{o}	110^{o}-120^{o}	90^{o}-110^{o}	120^{o}-130^{o}
Angulation distal end ventral ovipositor valve	shallow $> 120^{o}$	deep $< 100^{o}$	deep $< 100^{o}$	deep $< 100^{o}$

TABLE 9. Similarity of five species of Wernerella based on 14 morphological characters.

	pachecoi	sublaevis	sp.
sublaevis	10 (71%)		
sp.	2½ (18%)	4 (29%)	
picteti	3½ (25%)	3 (22%)	10½ (75%)

Characters were treated according to the methods of Lems and Holzapfel (1968). In cases of range overlap or overlap in non-numerical features, $\frac{1}{2}$ point was awarded. When species are compared two at a time, a table may be constructed which shows similarity of taxa based on the characters studied (Table 9).

Wernerella pachecoi and sublaevis closely resemble each other; likewise, picteti and W. sp. have many morphological features in common. W. sp. and picteti are the only two species that have clear hyaline wings; it is interesting that both have western distributions.

Since pachecoi has a wide distribution in North Africa and is found on Lanzarote and Fuerteventura, the islands closest to the African coast, it is likely that this is the stem species of the Canarian Wernerella fauna. My data suggests that W. sublaevis represents pachecoi on Gran Canaria.

Furthermore, it is likely that the clear-winged picteti-W. sp. group was derived from the band-winged pachecoi-sublaevis complex. From the points of view of distribution and morphology, the most simple summary of relations between Wernerella species on the Islands may be summarized as follows: sublaevis diverged from pachecoi. W. sp. was derived from sublaevis, and underwent rather extensive differentiation on Gran Canaria, probably at high elevation in the Roque Nublo area, and then spread to lower elevations of similar ecology, as well as to Tenerife and Gomera, where the closely related picteti is now found.

MATERIAL STUDIED. W. pachecoi. FUERTEVENTURA: Playa Cofete 1 M, 4 ♂, 14 ♀ , UMMZ; Fraile-Jandia 150 M, 7 ♀ , UMMZ; Gran Valle 200 M, 2 ♂ , 9 ♀ , UMMZ; Boca mal Nombre 5 M, 5 ♂, 5 ♀ , UMMZ; Antigua 250 M, 2 ♂, 2 ♀, UMMZ; Playa Blanca 1 M, 3 ♂, 3 ♀, UMMZ; Correlejo 10 M, 1 ♂, UMMZ; Gran Tarajal 180 M, 3 ♂, Madrid; Rio Cabra 20 M, 2 ♂, Madrid; Taralejo 50 M, 2 ♀ , Madrid. LANZAROTE: Femés 150 M, 11 ♀ , 2 ♂, UMMZ; La Caleta 10 M, 1 ♀ , UMMZ; Antigua 30 M, 1 ♀ , UMMZ; Arrecife 10 M, 2 ♀ , Hamburg, 1 ♀ BMNH. Wernerella picteti. GOMERA: Cumbre Carbonera 630 M, 1 ♂, 3 ♀ , UMMZ. TENERIFE: Los Cristianos 10 M, 3 ♂, 6 ♀ , UMMZ; Barranco del Infierno 230 M, 3 ♂, 11 ♀ , UMMZ; Chio 800 M, 3 ♂, 1 ♀ , UMMZ; Santiago-Masca 975 M, 2 ♂, 2 ♀ , UMMZ; Masca 500 M, 1 ♀ , UMMZ; Medano 5 M, 7 ♂, 7 ♀ , Madrid; Guimar 300 M, 2 ♀ , Madrid. Wernerella sublaevis. GRAN CANARIA: Maspalomas 5 M, 4 ♀ , 1 ♂, BMNH; Puerto de la Luz 5 M, 3 ♂, 3 ♀, Madrid; Las Palmas 10 M, 3 ♀ , 1 ♂, BMNH; Barranco Balos Los Letreros, 1 ♀ , BMNH: Hoya de la Plata 10 M, 1 ♂, 1 ♀ , BMNH. Wernerella sp. GRAN CANARIA: Cruz de Tejeda 1450 M, 6 ♂, 5 ♀ , BMNH; Roque Nublo 1700 M, 3 ♂, 10 ♀ , BMNH, 3 ♂, 2 ♀, UMMZ; San Bartolomé 750 M, 1 ♂, UMMZ; Tazartico 640 M, 1 ♀ , UMMZ; San Nicolas 150 M, 1 ♂, 1 ♀ , UMMZ; Mogan 800 M, 1 ♂, 2 ♀ , UMMZ.

Family: Acrididae
Subfamily: Truxalinae
Species on the Canary Islands: Truxalis nasuta (Linnaeus, 1758)

Truxalis nasuta is a non-endemic species known from Gran Canaria and Tenerife of the Canary Islands. Its non-insular distribution is broad, extending throughout most of Africa and into the Mediterranean region of southern Europe (Map 18). The subfamily to which this species belongs contains only a few genera (Uvarov, 1966), which occur mainly in the tropical and subtropical grasslands of Africa.

I collected two nymphs of Truxalis nasuta in June, 1966, in a fallow field overgrown with grasses, crucifers and composites near the town of Mogan, Gran Canaria, at 770 meters elevation. I also found one adult female in a disturbed area near the capital of the island, Las Palmas, late in April. Gardner (1960) reports taking two males and one female of this species at Puerto de la Cruz, Tenerife.

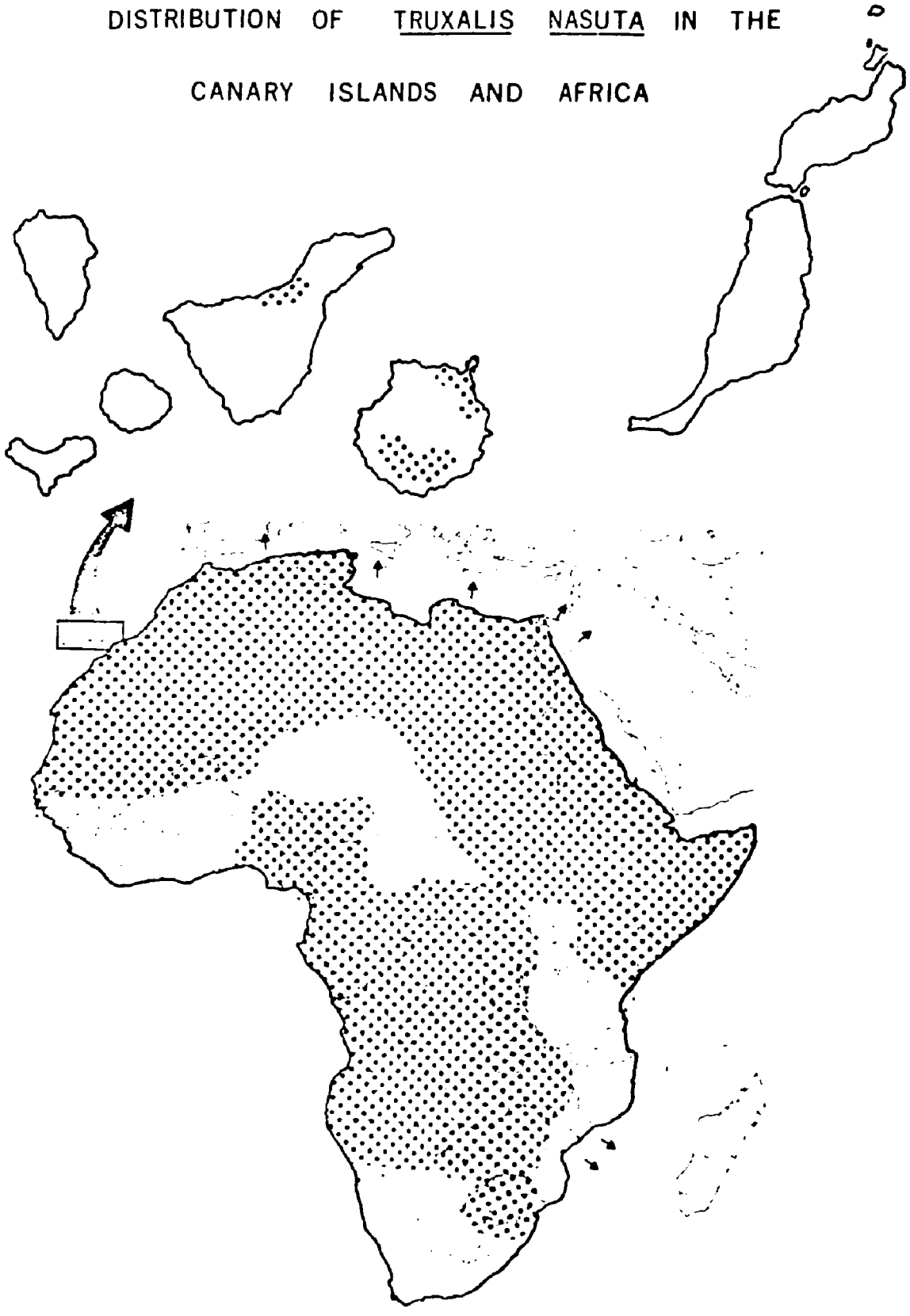
Family: Acrididae
Subfamily: Gomphocerinae
Species on the Canary Islands: Dociostaurus maroccanus (Thunberg, 1815)
Omocestus simonyi (Krauss, 1892)
Stenohippus bonneti (Bolivar, 1885)

Three species represent the very large subfamily Gomphocerinae on the Canary Islands: Dociostaurus maroccanus, Omocestus simonyi and Stenohippus bonneti. O. simonyi is an endemic species on the Islands; the other two species are non-endemic (Map 19).

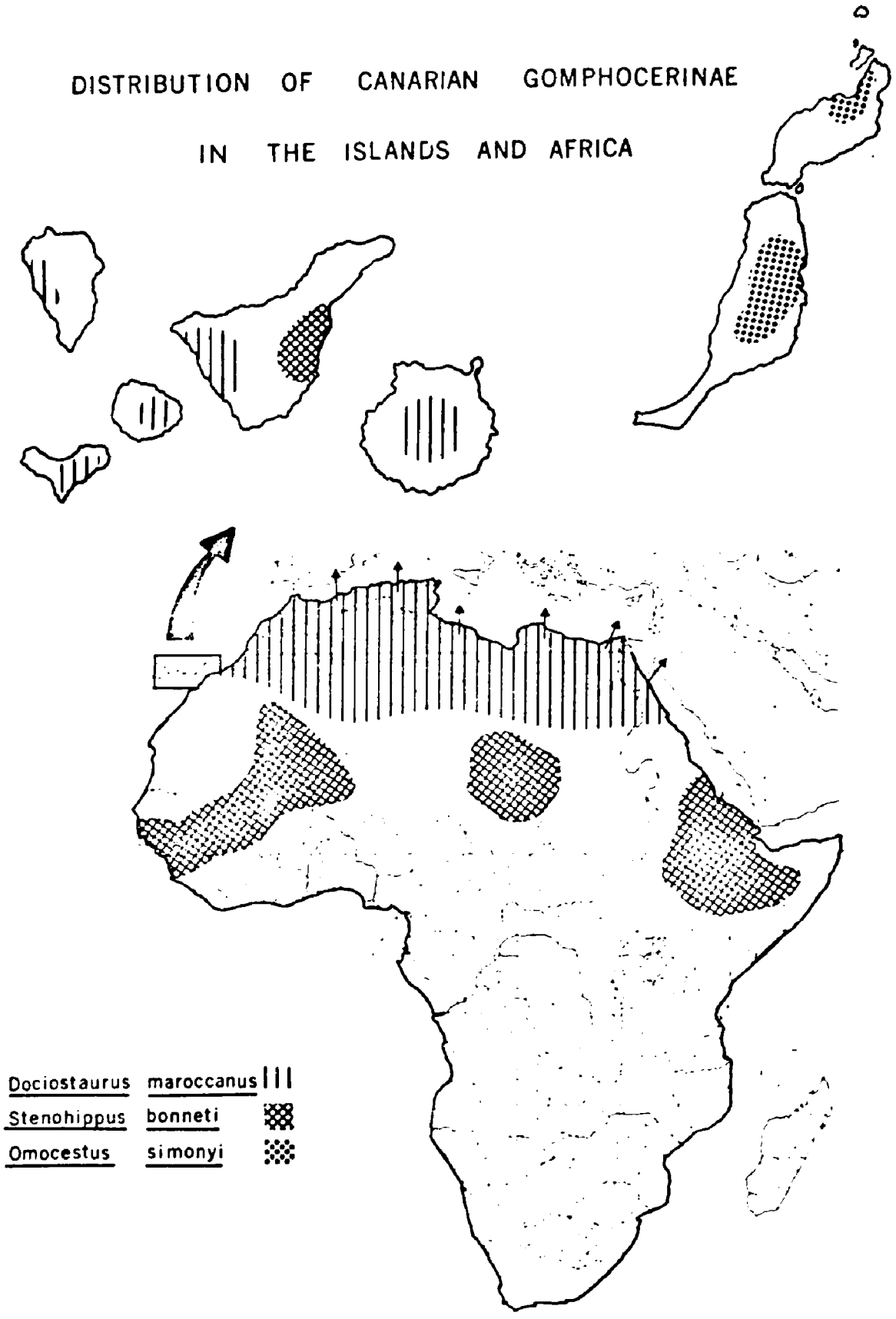
Stenohippus bonneti is known from Mali, Senegal, Ennedi,

MAP 18. Distribution of Truxalis nasuta in the Canary Islands and Africa.

DISTRIBUTION OF TRUXALIS NASUTA IN THE CANARY ISLANDS AND AFRICA



MAP 19. Distribution of the Canarian Gomphocerinae in the Islands and Africa.


DISTRIBUTION OF CANARIAN GOMPHOCERINAE
IN THE ISLANDS AND AFRICA
Dociostaurus maroccanus
Stenohippus bonneti
Omocestus simonyi

Ethiopea, and the Canary and Cape Verde Islands (Dirsh, 1968). On the Canaries, it has been reported several times from Tenerife (Willemse, 1936; Chopard, 1954), although I have seen none of this material.

Dociostaurus maroccanus undergoes phase changes similar to those so well-known in Schistocerca and Locusta. In the Canaries I have collected and seen only the solitaria form of this species, easily distinguished from the gregaria form by the sharply defined X on the dorsum of the pronotum (Chopard, 1943). This species is known from five of the Islands (Map 19), as well as from localities in southern Europe, southwestern Asia, North Africa and Madeira. Chopard (1943) reports that in Africa it tends to reproduce on high plateaus. I have collections of this species from all five islands with the exception of Hierro; all collections were made above 400 meters. Although the vegetation at the collection sites varied (Table 10), the localities were all characterized by weedy, open vegetation.

Studies of the internal genitalia of males from La Palma and Gran Canaria, and external genitalia of females from Tenerife, La Palma and Gran Canaria, indicate that divergence into insular morphs has not occurred in this group on the Islands.

Eight species of Omocestus are known from the North African region. Two of these, O. lucasii (Brisout, 1851) and raymondi (Yersin, 1863), are also known from southern Europe.

Stenobothrus simonyi was described by Krauss in 1892. Karny,

TABLE 10. Vegetation at collection sites of Dociostaurus maroccanus on the Canary Islands.

Plant species	Life form	Family	C Roque Nublo area - 1500M	T Masca 1050 M	G Tagamiche trail 950 M	P Lomo Caballo 580 M
Cistus monspeliensis	N	Cista.			2	
Echium decaisnei	N	Borag.	2			
Echium onosmaefolium	N	Borag.	1			
Euphorbia regis-jubae	N	Eupho.		+	1	
Inula viscosa	N	Compo.		+		
Rumex lunaria	N	Polyg.		+		
Salvia canariensis	N	Labia.	1			
Opuntia tuna	SS	Cacta.				+
Aeonium canariense	Ch	Crass.		+		
Andryala pinnatifida	Ch	Compo.			+	
Lavandula pinnata	Ch	Labia.		+		
Psoralea bituminosa	Ch	Legum.		+		+
Cynara cardunculus	H	Compo.				2
Notholaena vellea	H	Pteri.		+		
Orizopsis miliacea	H	Grami.		+		
Sanguisorba verrucosum	H	Rosac.				+
Anagallis arvensis	T2	Primu.	1			
Andropogon hirtus	T2	Grami.	1	2		1
Echium plantigineum	T2	Borag.			1	1
Galactites tomentosa	T2	Compo.	1	1		

TABLE 10. (Continued)

Avena barbata	Th	Grami.		+	1	1
Brachypodium distachyum	Th	Grami.	+			
Briza maxima	Th	Grami.			1	
Bromus rubens	Th	Grami.		+	1	2
Calendula arvensis	Th	Compo.	1			2
Chenopodium murale	Th	Cheno.	+			
Erodium chium	Th	Geran.	1	+	1	
Filago gallica	Th	Compo.	+			
Pallensis spinosa	Th	Compo.		1		1
Silene vulgare	Th	Caryo.	1			+
Trifolium arvense	Th	Legum.		+	+	1
Trifolium campestre	Th	Legum.				1

in 1907, relegated simonyi to the genus Chorthippus, and in 1910, Kirby included the species in the mainly African genus, Omocestus.

Omocestus simonyi is endemic to the Canary Islands. It was known only from Lanzarote until 1966, when I collected material at La Oliva and Antigua in Fuerteventura. On both islands, I found the species living in the semi-desert belt. The vegetation composition is largely annual, with shrubby and woody elements consisting mostly of weedy (Nicotiana glauca) and highly branched desert forms (Table 11).

Characteristics of internal and external male genitalia and of the external genitalia of females, as well as a variety of other morphological features, were studied in detail. Material from Lanzarote and Fuerteventura could not be distinguished on morphological grounds.

MATERIAL STUDIED. Dociostaurus maroccanus (UMMZ). LA PALMA: Barranco Izcagua 1250 M, 6 ♂, 3 ♀ ; El Paso 900 M, 3 ♂, 3 ♀ ; El Time 590 M, 1 ♂, 2 ♀ ; Lomo Caballo 580 M, 3 ♂, 4 ♀ . TENERIFE: Santiago-Masca 1050 M, 4 nymphs; Castillas 550 M, 1 ♀ , 5 nymphs; Barranco Igueste 400-500 M, 1 ♀ . GRAN CANARIA: Roque Nublo 1500 M, 3 ♂, 4 ♀ . GOMERA: Tagamiche 950 M, 15 nymphs. Omocestus simonyi. LANZAROTE: Haria 200 M, 4 ♂, BMNH, 1 ♀ , UMMZ; La Caleta, 1 ♀ , UMMZ; FUERTEVENTURA: La Oliva 280 M, 4 ♂, 7 ♀ ; UMMZ; Antigua 250 M, 1 ♀ , UMMZ; Above Ampuyenta 200 M, 3 ♂, 5 ♀ , BMNH; Puerto del Rosario 20 M, 4 ♀ , BMNH.

TABLE 11. Vegetation at collection sites of Omocestus simonyi on Fuerteventura and Lanzarote.

Plant species	Life form	Family	F Antigua 250 M	La Oliva 270 M	L La Caleta 5 M
Nicotiana glauca	M	Solan.	1	+	
Asparagus albus	N	Lilia.		2	
Kleinia neriifolia	N	Compo.	+	1	
Lycium afrum	N	Solan.		1	
Rubia fruticosa	N	Rosac.			
Caralluma burchardii	SS	Asclep.		+	
Aizoon canariensis	Ch	Aizoa.			1
Fagonia cretica	Ch	Zygop.		+	
Launaea spinosa	Ch	Compo.		+	
Lotus lancerottensis	Ch	Legum.	1	1	
Picridium ligulatum	Ch	Compo.	+	+	+
Plantago serraria	Ch	Plant.	1		
Stipa tortilis	H	Gram.	+	+	
Mesembryanthemum crystallinum	G	Aizoa.		1	1
Mesembryanthemum nodiflorum	G	Aizoa.	+	+	+
Echium plantagineum	T2	Borag.		1	
Linum strictum	T2	Linac.		1	
Sisymbrium erycimoides	T2	Cruci.	+		
Avena barbata	Th	Grami.	+	+	
Astragalis hamosus	Th	Legum.	+	2	+
Atractylis cancellata	Th	Compo.		+	

TABLE 11. (Continued)

Bromus macrostachys	Th	Grami.	+	+	
Calendula arvensis	Th	Compo.	+	+	1
Centaurea melitensis	Th	Compo.	+		
Chenopodium album	Th	Cheno.	2		
Filago gallica	Th	Compo.			+
Lamarkia aurea	Th	Grami.	+	+	+
Medicago minima	Th	Legum.			+
Picridium tingitanum	Th	Compo.		+	+
Rumex bucephalophorus	Th	Polyg.			1
Silene gallica	Th	Caryo.	+	+	
Sonchus bourgeaui	Th	Compo.	+	1	+
Tragus racemosus	Th	Grami.			1

CHAPTER TWO: THEORETICAL PROBLEMS IN THE ORIGIN, DISTRIBUTION, DIVERSITY AND SPECIAL ADAPTATION OF THE ACRIDOIDEA OF THE CANARY ISLANDS

Since the works of Darwin (1859) and Wallace (1892), it has been more or less taken for granted that remote oceanic islands have depauperate floras and faunas, and that they contain biotas with special adaptations not characteristic of mainland areas. In his comprehensive consideration of the distribution of organisms, Preston (1962) well states that one of the major difficulties in formulating a theory of distribution is that numerical data are scarce; in short "... Taxonomy is in bad shape..."

Many papers dealing with the theoretical aspects of distribution (Hamilton, et al., 1963-1967; Lack, 1944) have emphasized the Galápagos Archipelago for the simple reason that the flora and fauna of this island system are well known and their species may be numerically tabulated.

I believe that the Canarian Archipelago also falls into this category. The estimates of Lems (1960) of the vascular flora of the Canaries are essentially complete, excluding not more than 50 species, most of which are narrow endemics or recently introduced weeds. Data on the Acridoid fauna are now also complete enough to be subjected to numerical analysis.

Chapter Two deals with theoretical problems of faunal origins,

insular distributions and special adaptations of the Acridoidea of the Canary Islands. Number of species of both Acridoidea and vascular plants is correlated with topographic features of the Islands in an effort to achieve an understanding of the basis of the distribution of these groups.

I. Origin of the Canary Island Acridoidea.

Table 12 is a summary of the geographic distribution of the Acridoidea of the Canary Islands. The 20 species endemic to the Canaries represent a large fraction (43%) of the total fauna.[7] Seven species of the endemic taxa belong to Arminda, a genus of the Catantopinae. The remainder belong to the subfamilies Oedipodinae (6), Gomphocerinae (1), Pamphaginae (2), Dericorythinae (1), Calliptaminae (1), Eyprepocnemidinae (1), and to the Pyrgomorphinae (1).

Twenty-six non-endemic species are known from the Canary Islands. All of these taxa also occur in Africa. Of these, five, Dericorys lobata, Oedipoda fuscocincta, Sphingonotus lucasii, Wernerella aspera and Wernerella pachecoi are limited in distribution to northwestern Africa. A sixth, Stenohippus bonneti, has a somewhat disjunct range, stretching east to west across north-central Africa. We can conclude that at least these groups were probably introduced to the Canary Islands from the African continent.

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[7] Pyrgomorpha tereticornis and Oedipoda canariensis also occur in the Azores.

TABLE 12. Summary of the geographic range of Canarian Acridoidea

Species	Range			
	Canaries only	Africa	Europe	Asia
Purpuraria erna	+			
Acrostira bellamyi	+			
Dericorys lobata		+		
Dericorys minuta	+			
Pyrgomorpha cognata		+		+
Pyrgomorpha tereticornis	+*			
Calliptamus barbarus bar.		+	+	+
Calliptamus plebeius	+			
Eyprepocnemis cinerea	+			
Anacridium aegyptium		+	+	+
Schistocerca gregaria		+	+	+
Arminda brunneri	+			
Arminda burri	+			
Arminda fuerteventurae	+			
Arminda hierroënsis	+			
Arminda lancerottensis	+			
Arminda latifrons	+			
Chopardminda canariensis	+			
Acrotylus insubricus in.		+	+	
Acrotylus longipes		+	+	+
Acrotylus patruelis		+	+	+
Aiolopus strepens		+	+	+
Aiolopus thalassinus		+	+	+
Locusta migratoria		+	+	+
Oedaleus decorus		+	+	+
Oedaleus senegalensis		+		+
Oedipoda caerulescens		+	+	+
Oedipoda canariensis	+*			
Oedipoda fuscocincta		+		
Scintharista notabilis no.		+	+	
Sphingonotus caerulens		+	+	
Sphingonotus canariensis		+		+
Sphingonotus freyi	+			
Sphingonotus lucasii		+		
Sphingonotus rubescens		+	+	+
Sphingonotus savignyi		+		+
Sphingonotus willemsei	+			
Wernerella aspera		+		
Wernerella pachecoi		+		
Wernerella picteti	+			
Wernerella sp.	+			

TABLE 12 (Continued)

	Canaries only	Africa	Europe	Asia
Wernerella sublaevis	+			
Truxalis nasuta		+	+	+
Dociostaurus maroccanus		+	+	+
Stenohippus bonneti		+		
Omocestus simonyi	+			
Totals	20	26	16	17

* Also known from the Azores.

A seventh taxon, Scintharista notabilis notabilis, has a mainly North African distribution, with a narrow extension into the southern portion of the Iberian Peninsula (Uvarov, 1941).

A number of other species have North African distributions, but are also known from Europe and/or Asia. Notable examples are Calliptamus barbarus barbarus (Map 5), Acrotylus insubricus insubricus (Map 10), Oedipoda caerulescens (Map 14), and Dociostaurus maroccanus (Map 19). Furthermore, species known from southern Africa, as well as the Canary Islands, are also widely distributed in northwestern Africa. Schistocerca gregaria (Map 8), Acrotylus patruelis, Acrotylus longipes (Map 10), Aiolopus thalassinus (Map 11), Locusta migratoria (Map 12) and Truxalis nasuta (Map 18) have this pattern of distribution.

The problem of origins of the Acridoid fauna in cases where species are known also from Europe and/or Asia is complex. Twelve species from the Canaries are known from southern Europe, Asia and Africa, three additional species found on the Canaries are distributed in Africa and Europe, but not Asia, and four taxa are found in Asia and Africa, but not in southern Europe. Before the geographic origin of the Canarian populations of these species can be ascertained with any degree of certainty, specimens from all parts of the geographic ranges must be studied, and their pertinent zoogeographic history must be determined from the beginning of the Tertiary. These requirements are beyond the scope of this project.

The Iberian Peninsula of southern Europe would be expected to be of importance in contributing to the Acridoid fauna of the Canaries. Several reasons come to mind. Before joining the North Equatorial Current in the Atlantic Ocean, the Canarian Current sweeps by the western coast of the Peninsula, as well as past the northwestern coast of Africa and the Canary Islands (Coker, 1947). Debris moving along this aquatic system might be expected to carry some forms. Other than Africa, the Iberian Peninsula is the closest land mass to the Canary Islands. Representatives of a given species widely distributed on the Peninsula would be expected to have a better chance of reaching the Islands than a similar population in southern Africa or Asia. Morales Agacino (1942) presented a summary of the locusts and grasshoppers of the Iberian Peninsula. A comparison of the species on his list with a list of Canarian Acridoid species indicates that, with the exception of Acrotylus longipes, all species known from Europe occurring on the Canaries are also found on the Iberian Peninsula. Further, the center of evolution of at least Omocestus and Oedipoda seems to be southern Europe. Thirteen species of Omocestus are known from the Iberian Peninsula as compared with only seven from the whole of Africa (Dirsh, 1965); six species of Oedipoda are known from the Iberian Peninsula as compared with only four from the African continent.

The North African-Iberian-Mediterranean affinities of the Acridoid fauna of the Canary Islands are paralleled by the affinities of

the vascular flora of the Islands. Lems (1958, 1960) concludes that the majority of the vascular flora of the Canaries was derived from species that had a mainly North African-Mediterranean distribution in the Cretaceous, or possibly Jurassic.

The core of the endemic flora of the Canary Islands belongs to the geographic classification proposed by Christ, the "Ancient African" (Christ, 1892). This element supposedly was once nearly continuous throughout the greater portion of Africa, but was disrupted during the formation of the Sahara desert as well as by the expansion and contraction of the tropical rain forest. At the present time, the remnants are found around the periphery of the continent. Euphorbia regis-jubae, Dracaena draco, Prenanthes pendula and a score of other species fall into this classification.

The Sahara desert itself has contributed Launaea, Phoenix and Tamarix to the Canarian flora. Lems (1958) concludes that these introductions were probably recent since most species cannot be distinguished from their African counterparts. Much of the littoral element of the Canary Islands is of African and occasionally European origin, including members of the genera Crithmum, Limonium and most of the Chenopodiaceae.

The present Mediterranean flora has contributed to the Canaries a few species which are particularly well adapted to long-distance dispersal (Olea, Juniperus, Pistacea). Canarian species of Cytisus, Spartosytisus, Adenocarpus and Cistus appear to be distantly related to

the Mediterranean ericoid-leguminose shrubs. A third group with Mediterranean relations is introduced weeds.

The correspondence of fossils of southern Europe, Spain and Italy implicate this geographic area with the origin of the Canarian laurel forest; this element of Tertiary rain forest was also probably distributed in North Africa during the Miocene and Pliocene (Lems, 1960).

II. Distribution of species of Acridoidea on the Islands.

The known distribution of each species of Acridoidea on the Canary Islands is indicated in Table 13. The Acridoid fauna is most diverse on Gran Canaria and Tenerife, two of the three large islands in the archipelago (Table 21, p. 165), an observation which will be discussed in detail in a later section. The fauna is relatively impoverished on the eastern islands, Lanzarote and Fuerteventura, and becomes increasingly so west of Tenerife.

Although there are only 46 species of Acridoidea on the Canaries, these taxa are members of a broad range of higher categories: 3 families and 10 subfamilies. Furthermore, there are 22 genera found on the Islands, many of which are represented by only a single species. Arminda, Sphingonotus and Wernerella are the only genera with more than three species each on the Islands, and all three genera have Canarian endemic members. On the other hand, parallel nonendemic genera are usually represented in Africa by more than 5 species and

TABLE 13. Distribution of species of Acridoidea on the Canary Islands.[#]

Family Subfamily	Species	L	F	C	T	G	P	H
PAMPHAGIDAE								
Pamphaginae	Acrostira bellamyi					+*		
	Purpuraria erna		+*					
PYRGOMORPHIDAE								
Pyrgomorphinae	Pyrgomorpha cognata				+			
	Pyrgomorpha tereticornis			+*				
ACRIDIDAE								
Dericorythinae	Dericorys lobata	+	+					
	Dericorys minuta			+*				
Calliptaminae	Calliptamus barbarus	+						
	Calliptamus plebius			+**	+**	+**	+**	+**
Eyprepocneminae	Eyprepocnemis cin.			+**	+**			
Cyrtacanthacridinae	Anacridium aegyptium			+				
	Schistocerca gregaria	+	+	+	+	+		
Catantopinae	Chopardminda canariensis			+*				
	Arminda brunneri				+**		+**	
	Arminda burri			+**	+**			
	Arminda hierroënsis							+*
	Arminda fuerteventurae		+*					
	Arminda lancerottensis	+*						
	Arminda latifrons					+*		
Oedipodinae	Acrotylus insubricus	+	+	+	+	+	+	
	Acrotylus longipes	+		+		+		
	Acrotylus patruelis	+	+	+	+	+	+	+
	Aiolopus strepens			+	+	+	+	+
	Aiolopus thalassinus	+		+	+	+	+	+
	Locusta migratoria			+	+	+	+	
	Oedaleus decorus				+			
	Oedaleus senegalensis						+	

TABLE 13 (Continued)

Family Subfamily	Species	L	F	C	T	G	P	H
	Oedipoda caerulescens			+	+			+
	Oedipoda canariensis			+**	+**			
	Oedipoda fuscocincta				+?			
	Scintharista notabilis			+	+	+	+	
	Sphingonotus canariensis	+	+	+	+	+		
	Sphingonotus caerulens	+	+	+	+	+	+	+
	Sphingonotus freyi			+*				
	Sphingonotus lucasii				+			
	Sphingonotus rubescens				+			
	Sphingonotus savignyi	+	+	+	+			
	Sphingonotus willemsei				+*			
	Wernerella aspera	+			+?			
	Wernerella sp.			+*				
	Wernerella pachecoi	+	+					
	Wernerella picteti				+**	+**		
	Wernerella sublaevis			+*				
Truxalinae	Truxalis nasuta			+	+			
Gomphocerinae	Dociostaurus maroccanus			+	+	+	+	+
	Omocestus simonyi	+**	+**					
	Stenohippus bonneti				+			
	Total species per island:	14	11	25	27	15	11	8

Islands abbreviated by first letter.

* Single island endemics.

** Endemic, but to more than one island.

often more than 10 (Table 14). Table 14 compares the number of species in genera common to the Canary Islands and to Africa. These data point to the conclusion that the Canarian Acridoid fauna is a rather incomplete representation of at least this mainland counterpart.

According to MacArthur and Wilson (1967), there is a tendency towards loss in absolute numbers of both species and higher taxa during dispersal along island chains as compared with mainland areas. Gressitt (1964) studied the Arthropod fauna of Antarctica and several subantarctic islands, Aucklands, Campbell and Macquarie, and reported a total of less than 1000 species. On Campbell Island he found 381 species of land Arthropods belonging to 138 families and 280 genera. An average of 1.4 species per genus represents a very diverse fauna. On individual islands in the Canaries, the species to genus ratio ranges from 1.1 on Hierro to 1.6 on Tenerife and Gran Canaria (Table 15, p. 141).

Neither Table 14 nor the statistics of Gressitt take area into account in comparing island and mainland faunas. However, Grant (1966) showed that the number of land birds per genus on the Tres Marias Islands is significantly less than on the equivalent area of the adjacent Mexican coast.

The comparison of species per genus number on island and mainland areas is ecologically interesting, but such comparisons are at least partly vitiated by the consideration that islands, surrounded by water, differ ecologically from mainland environments in important

TABLE 14. Comparison of species number of Acridoidea in the Canary Islands and Africa.

Genera in common to the Canaries and Africa	Number of species in Africa*	Number of species in the Canary Islands
Dericorys	6	2
Pyrgomorpha	20	2
Calliptamus	5	2
Eyprepocnemis	10	1
Anacridium	9	1
Schistocerca	1	1
Acrotylus	36	3
Aiolopus	10	2
Locusta	1	1
Oedaleus	16	2
Oedipoda	4	3
Scintharista	6	1
Sphingonotus	31	7
Wernerella	3	5
Truxalis	11	1
Dociostaurus	3	1
Stenohippus	8	1
Omocestus	7	1
TOTALS:	187	37

* Estimates based on data from Dirsh (1965).

respects. For example, simply the thermal buffering effect of the ocean gives Lanzarote a climatic stability in strong contrast to a desert area of equal size in the Spanish Sahara, a region which approximates Lanzarote in vegetation structure.

With the exception of the remote island, Hierro, with a total Acridoid fauna of only 8 species, the proportion of congeneric Acridoid species is approximately the same for all of the Canary Islands, regardless of size (Table 15). Grant (1966) implied that the size of an island tends to influence the number of its congeneric species, the larger the island the more congeners, resulting from the influences of amount and variety of resources available. Such a conclusion is not appropriate in the present case.

TABLE 15. Proportion of congeneric species of the total Acridoid fauna on the Canary Islands.*

Island	L	F	C	T	G	P	H
Total species	14	11	25	27	15	10	8
Congeneric species	8	5	15	17	7	4	2
% congeners	57	44	60	62	47	40	25
Mean species per genus	1.5	1.4	1.6	1.6	1.5	1.2	1.1

* Islands abbreviated to first letter.

A survey of the insular distribution of endemics presents several interesting relationships (Table 16). Based on its total fauna of 14 species, Lanzarote, one of the two islands close to Africa, has the lowest proportion of endemic species (14%). With the exception of Gran Canaria which has a percentage endemism of 40, the endemic Acridoid fauna of all other islands is approximately 25% (Fuerteventura 27%, Tenerife 23%, Gomera 27%, La Palma 20%, and Hierro 25%).

The richness of the endemic Acridoid fauna of Gran Canaria may be due to several things. First, and foremost, its most characteristic substrate is open lava, a preferred substrate for a large number of grasshopper species. Unlike the western islands of Tenerife, Gomera and La Palma, there are almost no traces of the forested areas which support fewer Orthopteran species than open lava. Secondly, the dissected topography of Gran Canaria affords possible geographic barriers to evolving populations. Thirdly, Gran Canaria is one of the largest of the Canary Islands, and fourthly, it is centrally located, possibly facilitating exchange of species with other islands.

Table 16 also indicates that Tenerife shares most endemics with other islands, although it has only one species which is endemic to it alone (Sphingonotus willemsei of the Cañadas region). Tenerife shares endemic Acridoidea with Gran Canaria (4 species), Gomera (2 species), La Palma (2 species) and Hierro (1 species). In fact, Tenerife shares an endemic with every island except the eastern ones, Lanzarote and Fuerteventura. The failure of Tenerife to share

TABLE 16. Statistics on endemism of the Acridoid fauna of the Canary Islands.*

	Island							
	L	F	C	T	G	P	H	Total species
Total species of Acridoidea	14	11	25	27	15	11	8	46
Species endemic to a single island	1	2	6	1	2	0	1	13
Species endemic, but on more than one island**	1	1	4	6	2	2	1	7
Nonendemic species	12	8	15	20	11	9	6	26

* Island names symbolized by first letter.

** Pyrgomorpha tereticornis and Oedipoda canariensis are also known from the Azores.

endemics with the eastern islands may, in part, be a function of distance, as well as related to differences in ecology.[8]

The distribution of endemic Acridoidea on and between islands is allopatric. In only two cases is more than one species of a genus established on any given island, and in these the species have allopatric distributions on that island. Wernerella sublaevis and W. sp. are both found on Gran Canaria; however, the former is a sandy-beach dweller, while W. sp. is found at high elevations. Similarly, Arminda (Chopardminda) canariensis and Arminda (Arminda) burri are both established on Gran Canaria. A. canariensis is found above 600 meters, and burri is known from the low-elevation semidesert region.

The tendency towards allopatry among the Canarian endemic taxa may be a response to competition for ecological resources. Elton (1946), Lack (1944) and others presented evidence suggesting that congeneric species are more similar ecologically than heterogeneric species. This is probably because the congeneric species possess more similar adaptive systems than the heterogeneric ones (cf. Lack, 1965). The allopatric distribution of endemics is particularly interesting when it is realized that there are many habitats in which Arminda, for example, would be expected to survive, but simply is not present. This observation may relate to annual fluctuations in

[8] Unlike Tenerife, Lanzarote and Fuerteventura house mainly a semidesert and littoral flora. Furthermore, they share several species of Acridoidea found nowhere else on the archipelago, Dericorys lobata, Wernerella pachecoi and Omocestus simonyi.

numbers of individuals and seasonal movements of segments of populations. The center of abundance of species A may be in the valley of Haria during one season, only to be found in an ecologically similar, but geographically different region 10 years hence.

III. Vertical stratification of species on the Islands with respect to vegetation zones.

One of the characteristic features of montane oceanic islands is predictable pattern of climatic stratification. The Canary Islands are exposed to the northeast trade winds during most of the year and these winds are apparently the major factor determining the climate in all except the regions above 1500 meters. There the climate is largely affected by the counter-trade winds of the upper air layers (Ceballos and Ortuño, 1951).

Within the climatic systems dominated by the trade winds, a number of subregional climatic types may be distinguished: the area near sea level where condensation is infrequent, the north and northeast windward side on each island where condensation results in cloud formation and rain, and the leeward side of the islands where the air decreases in humidity as it descends the dry slopes. From the point of view of climatic stratification, then, the Canary Islands can be divided into four major areas:

1) Lowlands below 400 meters: climate with mild winters and warm, dry summers.

2) North and northeastern faces of mountains, 300 - 1500 meters, where cloud formation occurs. This region is rarely without moisture in the form of clouds, fog, or rain.

3) South and southwestern slopes, 300 - 1500 meters, with dry, warm to cool climate, depending on altitude.

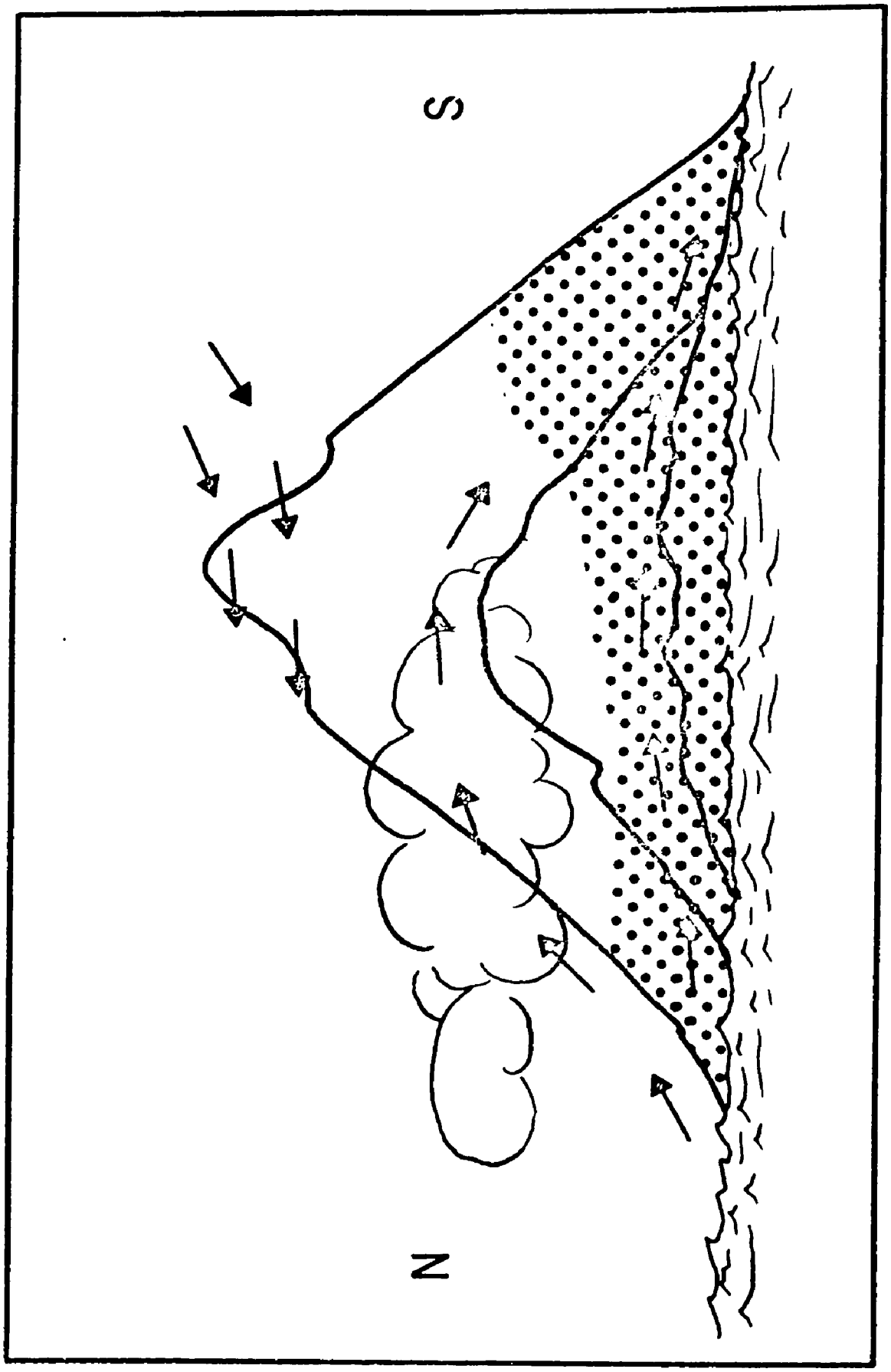
4) Highlands above 1500 meters, with dry counter-trade wind climate characterized by warm, dry summers and moist cool winters, with snow frequent above 2000 meters.

The relationship between elevation and climatic belts is shown in Figure 10 (modified from Lems, 1958).

Only the islands of Tenerife, Gran Canaria and La Palma possess all four of the climatic types. The other islands are not high enough to receive the effects of the counter-trade winds. On Gomera and Hierro, the clouds are not caught on the windward side of the island as they are in the above, but rather pour over the tops of the mountains, evaporating on the dry leeward sides. With the exception of the small Jandia ridge on southern Fuerteventura, Fuerteventura and Lanzarote are essentially without a cloud belt effect. These islands are simply too low for enough rising and cooling of air for cloud formation to occur.

There is a predictable relationship between climatic belt and vegetation type in the Canaries. Three major vegetation zones are recognized by Lems (1958), the basal xerophytic region (roughly corresponding to the lowland climatic belt below 300 meters), the forest

FIGURE 10. Relationship between elevation and climate in the Canary Islands. Arrows indicate wind direction. Stippling shows approximate area of the xerophytic zone. Low island represents either Lanzarote or Fuerteventura, island of intermediate elevation represents Gomera or Hierro. The tallest island may be Tenerife, La Palma or Gran Canaria.


S
N

region (300 - 1500 meters), and the subalpine region (above 1500 meters). Within these large belts are many communities of plants which Lems defines by methods described by Braun-Blanquet (1932).

For a variety of reasons, it is not feasible to attempt classification of the Acridoid species of the Canaries according to floristic communities. Many plant communities have not been described in the islands. Large portions of the southwestern portion of Gran Canaria have not yet been sufficiently investigated from the point of view of plant sociology to define floristic assemblages. Communities of plants are occasionally "out of place," following a stream bed or barranco into an unexpectedly low elevation. This may explain the large number of grasshopper species which share adjacent vegetation zones (Table 17).

Most investigators agree that most species of Orthoptera have rather well-defined ecological preferences. Cantrall (1943) found that the Orthopteran inhabitants of the E. S. George Reserve, Michigan, could be divided according to major ecological categories: dwellers in xeric, xeromesic and hydric environments. These three major habitats could then be further subdivided on ecological grounds. Cantrall observed that although certain taxa were restricted to specific habitats (Orchelimum campestre Blatchley), that others were generalized in preferences, occasionally changing habitat with seasonal advance (Melanopus femur-rubrum femur-rubrum).

In his study of the Alutacea group of the genus Schistocerca,

TABLE 17. Vertical distribution of species according to major vegetation belts.

Species	Open beach	Below 300 M Xerophytic	300-1500 M Forest	Above 1500 M Subalpine
Acrostira bellamyi			+	
Purpuraria erna			+	
Pyrgomorpha tereticornis	+	+		
Pyrgomorpha cognata	+	+		
Dericorys lobata	+	+		
Dericorys minuta	+			
Calliptamus barbarus		+		
Calliptamus plebeius		+	+	+
Eyprepocnemis cinerea	+			
Schistocerca gregaria		+	+	
Anacridium aegyptium		+	+	
Arminda brunneri		+	+	
Arminda burri		+	+	
Arminda fuerteventurae		+		
Arminda hierro'ensis		+		
Arminda lancerottensis		+		
Chopardminda canariensis			+	
Acrotylus insubricus	+	+	+	
Acrotylus patruelis	+	+	+	+
Acrotylus longipes	+	+		
Aiolopus strepens		+	+	
Aiolopus thalassinus		+	+	
Locusta migratoria		+	+	
Oedaleus senegalensis			+	
Oedipoda caerulescens		+	+	
Oedipoda canariensis		+	+	
Scintharista notabilis		+	+	
Sphingonotus caerulens		+	+	
Sphingonotus freyi	+			
Sphingonotus canariensis		+		
Sphingonotus savignyi		+		
Sphingonotus willemsei				+
Wernerella pachecoi	+	+		
Wernerella sublaevis	+			
Wernerella picteti	+	+		
Wernerella sp.		+	+	+
Truxalis nasuta	+	+	+	
Dociostaurus maroccanus			+	
Omocestus simonyi		+		
	13	29	21	4

Hubbell (1960) classified the three taxa considered according to habitat. S. alutaceae exhibited the most narrow ecological range, being found mainly in shrubby, moist to wet situations. S. lineata seemed to be more plastic in habitat choice, being abundant in weedy thickets in some areas, while in other areas, occurring in grassy dunes and open beach vegetation.

Tables 3, 4, 6, 10 and 11 indicate that among Acridoid species on the Canaries for which floristic data were prepared, species tend to be found in a particular structural type of vegetation, if not associated with a specific floristic community. For example, Calliptamus plebeius tends to be found in shrubby habitats, while Omocestus simonyi and Dociostaurus maroccanus tend to be found in annual, weedy areas.

Since the major vegetational belts recognized by Lems (1958) may be described by definite ecological parameters including not only temperature, rainfall and physical features of the substrate, but also the structural growth forms of the plants therein, I have chosen to examine the vertical distribution of the Acridoidea of the Canary Islands according to this classification. To these vegetational belts, listed on page 146, I have included one additional division to differentiate between those species found on sandy beach as distinct from those found in typical xerophytic scrub.

As indicated in Table 17, the majority of Acridoid species are found below the subalpine belt, and the Acridoid fauna is most diverse between the xerophytic belt and 1500 meters. Only four of the 39

species listed are found above 1500 meters: Calliptamus plebeius, Acrotylus patruelis, Sphingonotus willemsei and Wernerella sp. Three species are unique to the open beach: Dercorys minuta, Eyprepocnemis cinerea and Sphingonotus freyi, six species characterize the xerophytic belt: Calliptamus barbarus, Sphingonotus canariensis, Sphingonotus savignyi, Wernerella pachecoi, Wernerella sublaevis and Omocestus simonyi. Six species are found only in the forest region: Acrostira bellamyi, Purpuraria erna, Chopardminda canariensis, Oedaleus senegalensis, Oedipoda caerulescens and Dociostaurus maroccanus. A single species is an indicator of the subalpine zone, Sphingonotus willemsei. If a taxon is found in more than one vegetation zone, the zones are always adjacent; in no case is a species adapted to non-contiguous zones.

It is interesting that the only species found in all of the vegetation belts (Acrotylus patruelis) is also one of two species known from all seven of the Canary Islands. This species appears to be of high ecological valence on the mainland as well, occurring widely in Africa, southern Europe and southwestern Asia. Morales Agacino (1942) indicated that the species is nearly ubiquitous on the Iberian Peninsula. With the exception of Wernerella sp., species occurring on a single island are found in no more than two vegetation zones. Only species found on five or more islands occur in three or more vegetation belts.

Chopard (1937) classified the Orthopteran fauna of Madeira according to a vertical scheme: littoral zone, sandy area on the

eastern point of the island, cultivated zone to at least 800 meters, heath-pine to 1000 meters, laurel forest on the north coast to 1500 meters, and the high mountain zone over 1500 meters. Madeira is particularly difficult to study from an ecological point of view because of the tremendous disturbance by man; only the high mountain areas remain relatively untouched. Only four species of Acridoidea were included in Chopard's classification of Madeiran Orthoptera. Aiolopus thalassinus, known from the xerophytic and forest belts in the Canaries, is found in the cultivated zone in Madeira. Oedaleus decorus, not included in my classification because of conflicting data, is reported by Chopard from the high mountain zone on Madeira.

IV. Relationship between number of species and number of Islands.

Table 18 is a summary of the number of Acridoid species occurring on one, two, three, four, five, six and all seven of the major Canary Islands. This table was prepared in order to obtain further insight into the range of distribution of species on the islands, the way in which range is correlated with endemism, and to possibly give some information on the age of the fauna.

Twenty-two of the 46 known species occurring on the Canaries are known from a single island. These 22 represent 13 genera and 8 subfamilies. Of the 22 species known from only one of the seven islands, 13 are endemic to the Canaries (59%). The remaining nine species are nonendemic taxa.

TABLE 18. Number of species on consecutive numbers of islands.

Number of islands	Number of species	Number of genera	Number of subfamilies	Percent endemics
1	22	13	8	59
2	10	7	6	60
3	2	2	1	0
4	3	3	1	0
5	5	5	4	20
6	2	2	1	0
7	2	2	1	0

Ten species are known from two of the Canary Islands. These 10 represent seven genera and six subfamilies. Six of these species are endemic to the islands (60%). In every case, endemic species occur on adjacent islands (Table 13).

Of the species found on more than two islands, only one is endemic to the Canaries (Calliptamus plebeius Walker). All other taxa found on multiple islands are widely distributed on the mainland. Most species of Acridoidea found on more than two islands belong to the subfamily Oedipodinae (11). The subfamilies Calliptaminae (1), Gomphocerinae (1) and Cyrtacanthacridinae (1) are also represented in this group.

Several conclusions may be drawn from considering the numerical distribution of species on the Canaries. It is likely that non-endemic species found on a single island are relatively recent invaders to the Canaries. This is certainly so for Anacridium aegyptium which was not known from the Canaries until 1960, although it is widely distributed in Africa, Europe and Asia and has been known from the more northern Madeira Islands for many years. I would expect this generalization to hold particularly for those species with wide distributions on mainland areas, implying either high vagility or generalized ecological preferences.

The observation that distance from the mainland per se, a measure of isolation discussed in detail in section VI, has essentially no effect on numbers of species present on an island supports the

contention that much of the Acridoid fauna is rather new; it is, in fact, very possible that these islands do not represent barriers to distribution at all for many species, particularly for those strong fliers for which extended flights are characteristic. The most remote island in this chain, La Palma, is only about 280 miles from the west coast of Africa.

Furthermore, the low proportion of island endemics present on more than a single island, may point to the same conclusion, that the majority of the Acridoid fauna is rather new and as of yet, relatively undifferentiated. For example, seven species of Arminda are found on the Canary Islands; all are established on only a single island. However, two specimens of the genus have been taken on adjacent islands as erratics. In the large series of Arminda that I had available for study I found one specimen of A. burri from Tenerife. The species was known previously from only the adjacent island, Gran Canaria. Similarly, a single specimen of A. brunneri has been noted from La Palma (Holzapfel, 1971); this species was previously recognized as a narrow endemic of Tenerife. Not only in this case, but in every case, endemic species are known only from adjacent islands. In no instance is there a broad disjunction in a species distribution, for example between Hierro and Gran Canaria, two islands which share many ecological features. Broad disjunction may suggest a relict history. I interpret the observations in Arminda as possible expansion of ranges on the islands, which after a long history of introduction and

exchange with other islands, could result in sympatric distribution as the rule, rather than the exception.[9]

In addition to these characteristic adjacent distributions in endemics, there is no evidence of differentiation into subspecific status in any of the endemic taxa of Acridoidea. Omocestus simonyi, Wernerella picteti, Arminda brunneri, Arminda burri and Calliptamus plebeius were carefully studied for morphological differentiation. All results support this conclusion.

V. Winglessness and the Acridoidea of the Canary Islands.

The notion that aptery in insects is related to windiness and other features of oceanic islands has been maintained since the days of Darwin (Darwin, 1859; Carlquist, 1968). Most recently Gressitt (1964) has correlated the high ratio of flightless micropterous insects on Campbell Island with the windy nature of the island. Since a rather

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[9] I have been impressed with the allopatric distribution of the Orthoptera in the Canary Islands. In regard to the observation that in only two cases are more than a single endemic of a given genus found on one island, the generalization holds for the Tettigoniine genus Calliphona on the Canary and Madeira Islands. Three species of Calliphona are known from the Canary Islands: konigi, a short-winged form from the island of Tenerife, palmensis, a katydid with intermediate wing length from the island of La Palma, and a long-winged species C. alluaudi known from two islands in the chain, Gomera and Gran Canaria. Again, all populations are strictly allopatric. Furthermore, although the shape and sculpturing of the tenth tergite of male alluaudi from the two islands has undergone some differentiation, individuals of the species overlap in all other morphological characters, and cannot be distinguished on morphological grounds (Holzapfel and Cantrall, 1971).

large proportion of the Canarian Acridoid fauna is wingless, a study of factors influencing wing length in insects and a comparison of the proportion of aptery and microptery in taxa common to both the Canary Islands and Africa were considered to be in order.

There is much evidence from a variety of insect groups (Coleoptera, Lepidoptera, Odonata, Orthoptera and Diptera) that many factors may influence wing length. In many groups, there seems to be a correlation between development of adaptations which reduce dispersal ability and living in permanent habitats.[10] The ways in which dispersal is limited varies with the taxon under consideration. However, the adaptations tend to fall into two major categories: reduction in flying ability and increase in length of the life cycle. Jackson (1928), in a study of flight ability of water beetles, classified several hundred species from temperate regions of the world into the following categories: 1) inhabitants of permanent rivers, 2) lakes, 3) bog ponds and peat pools, 4) small ponds, 5) ditches, gravel pits and temporary artificial ponds. Sixty percent of the Carabid fauna of the permanent rivers were flightless, 23% of the lake fauna, 14% of the bog pond beetles, and 5% of the small pond category were unable to fly. None of the beetles found in the most temporary habitats including drainage

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[10] A permanent habitat is defined as one which would remain unchanged for thousands of years; for example, a large river or a climax vegetation type like the heath of the Canary Islands. This type of habitat is to be contrasted with a temporary habitat, such as a drainage ditch, or early successional stage in the vegetation of an area.

ditches, gravel pits and artificial ponds were flightless.

Data presented by Darlington (1943) suggest that the montane Carabid fauna of the Greater Antilles has a high percentage of wingless forms when compared with the fauna of low elevation islands in the same area. Darlington correlates this observation with the presence of stable vegetation belts in the mountainous regions as contrasted with deciduous, less persistent vegetation types on the lower islands. Lems (1958) has shown that although the forest region of the Canaries is characterized by a small number of stable, climax communities (laurel forest, heath and pine), that definition of climax communities in the lowland areas is not only difficult, but perhaps inappropriate. Most of the lowland communities defined on sociological grounds have disjunct distributions, both on and between islands and, at best, represent discontinuous habitats when contrasted with the continuous distribution of forest communities.

Many investigators have related length of wing and flight ability to length of life cycle (Alexander, 1967; Jackson, 1928; Sellier, 1954; and others). Masaki and Oyama's experiments with the cricket Nemobius yezoensis in Japan summarizes the implications of these reports (1963). Nemobius yezoensis normally overwinters as a late nymph in Japan, and is an adult early in the summer. It is the only cricket in Japan that overwinters in a stage more advanced than the egg, and the only cricket in Japan in which only micropterous forms are known naturally. Photoperiodic studies of development of eggs of

this species oviposited in the laboratory showed that development during a long day of 15 hours of light is significantly more rapid than development under conditions of short day with 12 or fewer hours of light. Furthermore, in no case did individuals have long wings when reared under short day conditions which resulted in slow development. A high proportion of individuals developed long wings under long day conditions. Thus, in some insects, there is a correlation between length of time for development and length of wings.

Wing length in insects has also been related to population density (Fuzaeu-Braesch, 1961; Saeki, 1966), genetics (Sellier, 1954; Bowden, 1963; Prevosti, 1960), and temperature of the environment (Alexander, 1967).

From this very brief review of a rather complex problem, one is able to conclude that wing length in insects may be related to a variety of factors, many of which are probably interrelated in nature. Most factors are operative on mainland and insular areas alike, hence reduction in wing length as an "island syndrome" can be questioned.

In order to determine the relationship of wing length in the Canary Island and African Acridoid faunas, the proportion of long-winged to wingless and reduced-winged species in each area was determined. A species was considered to have reduced wing length if the hind wings were shorter than the abdomen. Data for the African fauna is based on Dirsh (1965), Johnston (1956), and secondary references noted by these authors.

Although this analysis may suffer from the error that the Acridoid fauna of the Canary Islands is better known than that of Africa, information on wing length was available for 1,427 species of Acridoidea from the whole of Africa. Of these, 631 or 44% are either entirely wingless or with reduced wings (Table 19). In contrast, only 9 or 19% of the 46 species of Acridoidea in the Canaries are wingless, and none have reduced wings (Table 20). If only the subfamilies of Acridoidea represented on the Canaries are compared with the same subfamilies from Africa, the proportion of wingless and reduced-winged species remains higher on the continent (33% as compared with 19% for the Canaries) (Table 20). Subfamilies with largely long-winged species in Africa (Oedipodinae, Truxalinae) are represented by long-winged species on the Canaries. Dericorys, the only genus in the Dericorythinae with strictly long wings, is the only genus in this subfamily known from the Canaries. As a result of this analysis, one can conclude that there are proportionally fewer wingless grasshoppers on the Canary Islands than on the African mainland.

Three of the wingless Canarian taxa, Purpuraria, Acrostira, and Chopardminda, are found only in the forest belt in the Canaries. The remaining wingless species in the Canaries, all belonging to the genus Arminda, are found below 1000 meters, most often in disturbed open or weedy areas. It is interesting that essentially no grasshoppers are known from the laurel forest, per se, and few inhabit permanent heath and pine in the Canary Islands, the specific kind of vegetation

TABLE 19. Wing length of Acridoidea of Continental Africa.

Family Subfamily	Number of Genera	Number of Species	Number of wingless and reduced wing	Number of long winged
ACRIDIDAE				
Dericorythinae	5	18	13	2
Romaleinae	3	5	5	0
Lithidiinae	4	12	11	1
Hemiacridinae	22	60	32	20
Tropidopidinae	10	34	8	10
Oxyinae	9	30	29	1
Captacridinae	9	57	20	28
Calliptaminae	7	62	0	43
Euryphyminae	21	69	14	29
Eyprepocnemidinae	16	80	16	19
Catantopinae	67	210	99	104
Cyrtacanthacridinae	16	48	1	47
Egnatiinae	3	9	0	9
Acridinae	89	350	52	274
Eremogryllinae	2	5	0	5
Truxalinae	49	160	26	138
PAMPHAGIDAE				
Echinotropinae	4	9	8	1
Porthetinae	14	43	43	0
Akincerinae	10	37	2	10
Pamphaginae	10	60	60	0
Choratyphyminae	1	9	?	?
Thericleinae	13	47	47	0
Euschmidinae	5	21	21	0
PNEUMORIDAE	5	37	37	0
CHARILAIDAE	4	5	5	0
LATHICERIDAE	4	5	5	0
PYRGOMORPHIDAE	40	150	78	55
LENTULIDAE	20	69	69	0
Totals:			631	796

TABLE 20. Comparative wing length of Acridoidea of the Canary Islands and Africa.*

Family Subfamily	Canary Islands			Africa		
	Number of genera	Number of wingless species	Number of long-winged species	Number of genera	Number of wingless and reduced wing	Number of long-winged species
Pamphagidae						
Pamphaginae	2	2	0	10	60	0
Acrididae						
Catantopinae	2	7	0	67	99	104
Acridinae	8	0	23	89	52	274
Calliptaminae	1	0	2	7	0	43
Dericorythinae	1	0	2	5	13	2
Truxalinae	4	0	4	49	26	138
Cyrtacanthacridinae	2	0	2	16	1	47
Eyprepocnemidinae	1	0	1	16	16	19
Pyrgomorphidae						
Pyrgomorphinae	1	0	2	40	78	55
Totals	21	9	37	299	345	682
Percent wingless species:		19			33	

* The Gomphocerinae are here included in the Truxalinae.

where high proportions of wingless species were noted by Darwin (1858) and Darlington (1943).

The entire subfamily to which Purpuraria and Acrostira belong is brachypterous, micropterous or apterous; the closest known relative of the Arminda-Chopardminda complex, Pezotettix Burmeister, 1840, is micropterous (Krauss, 1892). In view of the fact that the closest relatives of all wingless taxa are also wingless or micropterous on continental Africa, it seems evident that the apterous condition does not represent an adaptation to insular conditions in this fauna.

The wingless condition of Acridoidea of the Canaries does, however, seem to be related to degree of endemism. All of the wingless genera of Acridoidea present on the islands are endemic. On the other hand, none of the genera of winged grasshoppers on the Canaries are endemic, although 11 of the species are (Table 13). Moreover, all of the apterous species are established on single islands, whereas several of the winged endemic species occur on several or at least adjacent islands (Calliptamus plebeius Walker; Omocestus simonyi Krauss).

VI. Relationship between species diversity of Acridoidea, the vascular flora, and topographic features of the Islands.

Tables 21 and 22 summarize the statistics on the Acridoid fauna, vascular flora and physical features of the Canary Islands. These data were compared by means of regression analyses based on

TABLE 21. Statistics on the Acridoid fauna, vascular flora and physical features of the Canary Islands.

	Lanzarote	Fuerteventura	G. Canaria	Tenerife	Gomera	La Palma	Hierro
Total species Acridoidea	14	11	25	27	15	11	8
Total species vascular plants	366	348	763	1079	539	575	391
Topographic dissection	0.2	0.7	1.1	1.9	1.4	1.4	0.6
Highest elevation (meters)	670	807	1950	3711	1484	2493	1520
Surface area (sq. km)	873	1725	1534	2060	378	728	277
Area below cloud belt	873	1725	1030	1170	208	363	194
Area in cloud belt	0	0	470	445	170	260	82
Area above 1500 meters	0	0	34	445	0	105	1
Distance from mainland (km)	120	90	205	285	320	380	350

TABLE 22. Distances (in kilometers) between each of the Canary Islands.*

Lanzarote						
Fuerteventura	13					
Gran Canaria	171	85				
Tenerife	226	169	60			
Gomera	330	256	126	28		
La Palma	381	326	200	86	58	
Hierro	417	335	203	113	62	68
	L.	F.	C.	T.	G.	P.

* Determined by reconstruction from the Times Atlas of the World, Condensed Version, 1967.

least squares determinations, and the results were tested for statistical significance by means of F-tests. Coefficients of correlation are given in table 23. Coefficients of correlation with significance exceeding the 0.05 level are starred, and indicate correlations of predicted biological significance.

It has been observed by numerous investigators, that as horizontal distance from the mainland increases the absolute numbers of species on islands, or species diversity, decreases (Raven, 1935; Tatewaki, 1963; Carlquist, 1965; MacArthur and Wilson, 1967). This observation has been attributed to differential dispersal facility of species in the source fauna, reduced probability of any individual reaching a remote area as compared with a near area, and ecological paucity of small islands. For both the Canary Island Acridoid fauna and the vascular flora, the relationship between distance from the mainland and species diversity does not fit a negative linear slope, but rather increases initially, then drops precipitously in islands more distant than 280 kilometers from the African coast. The trends in this correlation are essentially identical in vascular plants and Acridoidea (Figs. 11, 12).

The central islands supporting rich biotas are, however, large islands (Table 21). The observation that there is often a predictable relationship between numbers of species and surface area on which they are found is well documented, and recently has been used to formulate a theory of biogeography of all island forms (MacArthur and

TABLE 23. Correlation matrix between Acridoidea, vascular plants and topographic features of the Canary Islands.

Variable								
Number species Acridoidea	1.							
Number species vascular plants	2.	0.888*						
Elevation (meters)	3.	0.624*	0.911*					
Topographic dissection	4.	0.580*	0.832*	0.877*				
Nearest neighbor (km)	5.	-0.268	-0.163	-0.003	-0.071			
Surface area (square km)	6.	0.688*	0.590*	0.398	0.331	-0.514		
Area below cloud belt (sq. km)	7.	0.359	0.152	0.057	-0.074	-0.575	0.885	
Distance from mainland (km)	8.	-0.096	0.287	0.568	0.554	0.680	-.502	-0.805

* $P < .05$

FIGURE 11. Species-distance curve for the Acridoidea of the Canary Islands. If plotted as a linear relation according to the equation $y = mx + b$, $b = 17.68$ and $m = -0.0079$. The coefficient of correlation is -0.096.

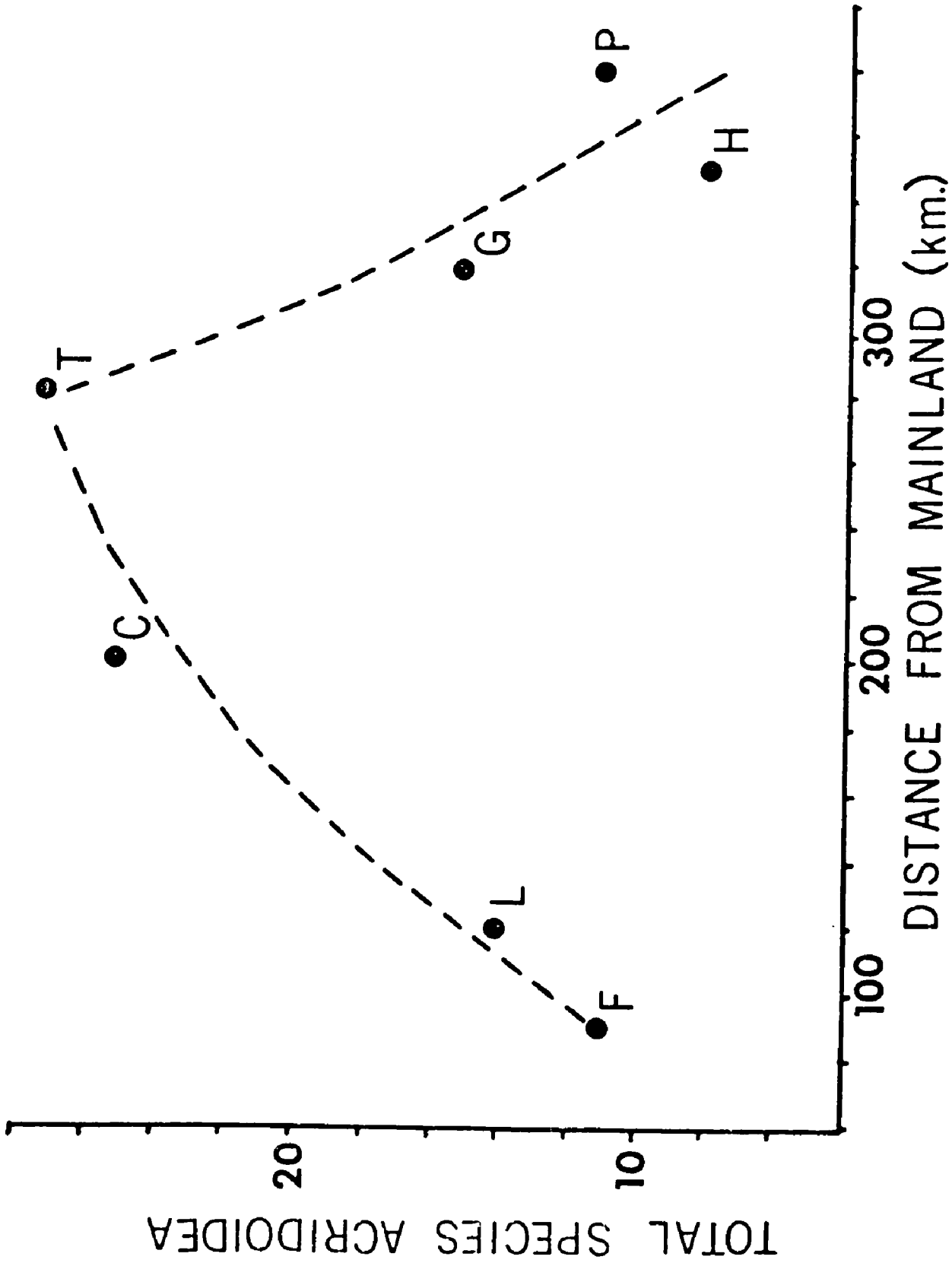
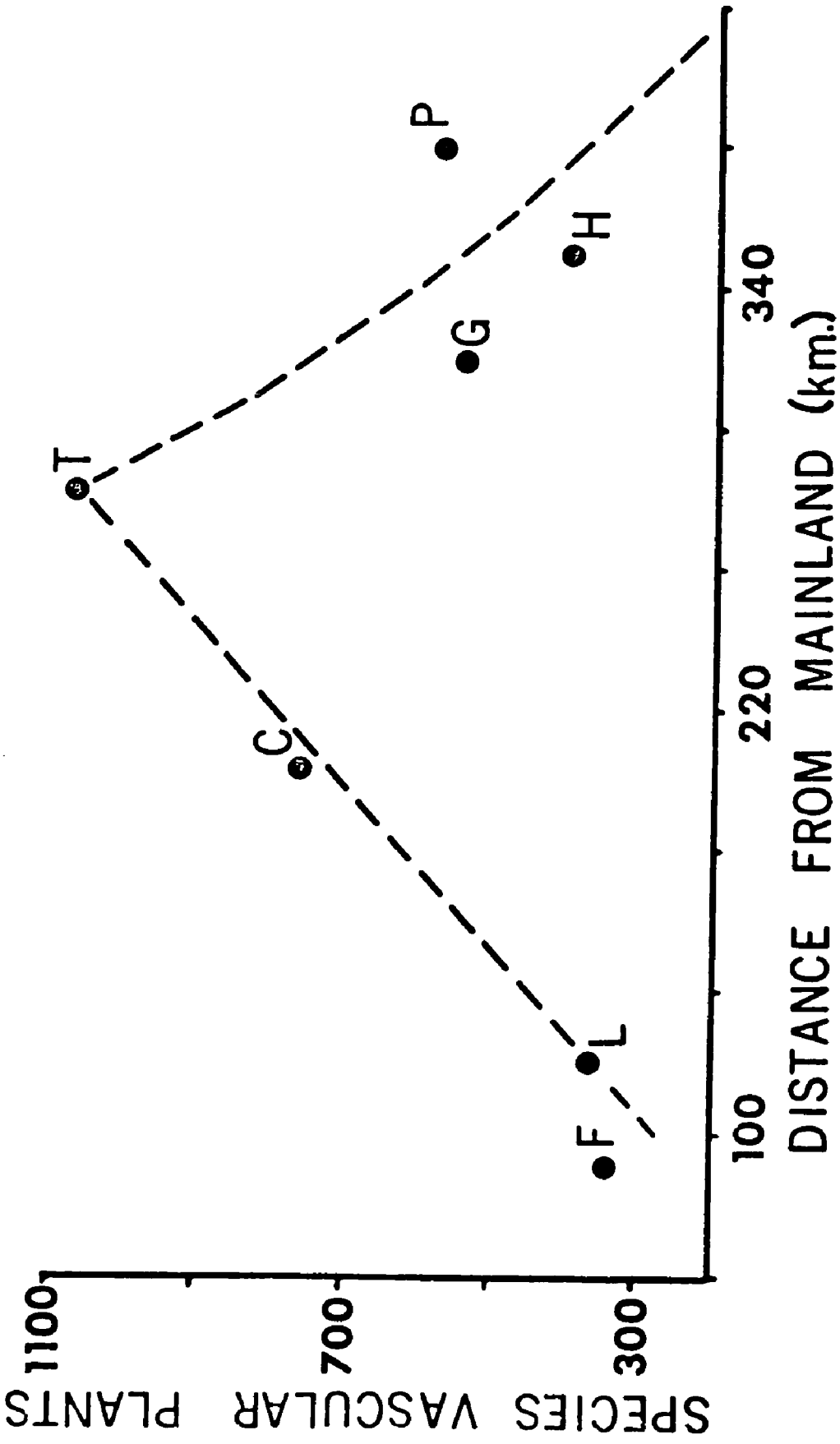

TOTAL SPECIES ACRIDOIDEA
20
10
100
200
300
DISTANCE FROM MAINLAND (km.)
P
H
G
T
C
L
F

FIGURE 12. Species-distance curve for the vascular flora of the Canary Islands. If plotted as a linear relation according to the equation $y = mx + b$, $b = 413.32$ and $m = 0.667$. The coefficient of correlation is 0.287.


SPECIES VASCULAR PLANTS
1100
700
300
DISTANCE FROM MAINLAND (km.)
100
220
340
P
H
G
T
C
L
F

Wilson, 1967). It is possible that if surface area were taken into account, the flora and fauna would conform to the predicted decrease in species diversity of distant islands.

Darlington (1957), in the herpeto-fauna of the West Indies, observed that dividing the surface area of the island by 10 divides the fauna by 2. Wilson (1961) has documented a similar system in which the number of ponerine ant species in Melanesia increases with area. His data add the additional interesting aspect that increase in number of species with area is more rapid on isolated islands or archipelagoes than in expanding sample areas taken on a single land mass. Greenslade (1967) has shown a close correlation between size of bird fauna and area of individual islands of the Solomon group.

Although Gran Canaria and Tenerife are indeed two of the three largest of the Canary Islands (Table 21), Fuerteventura, the third of the large island triplet, houses an impoverished flora and grasshopper fauna (Figures 13, 14).

Thus, neither size nor distance can explain the species diversity of taxa on the Canary Islands in entirety since Fuerteventura is not only the closest island to the mainland, but also is the second largest land mass in the archipelago.

Hamilton and Rubinoff (1963, 1964) have shown that distance from the nearest neighbor island inhabited by finches is important in explaining the variation in both total numbers of finch species on an island and number of endemics on an island. Nearest neighbor,

FIGURE 13. Species-area curve for the Acridoidea of the Canary Islands. The coefficient of correlation is 0.688. $z = 0.316$ where $S = CA^Z$ and where S is the number of species on an island, A is the surface area of the island, C is a constant, and Z is a measure of the faunal increase with size (MacArthur and Wilson, 1967).

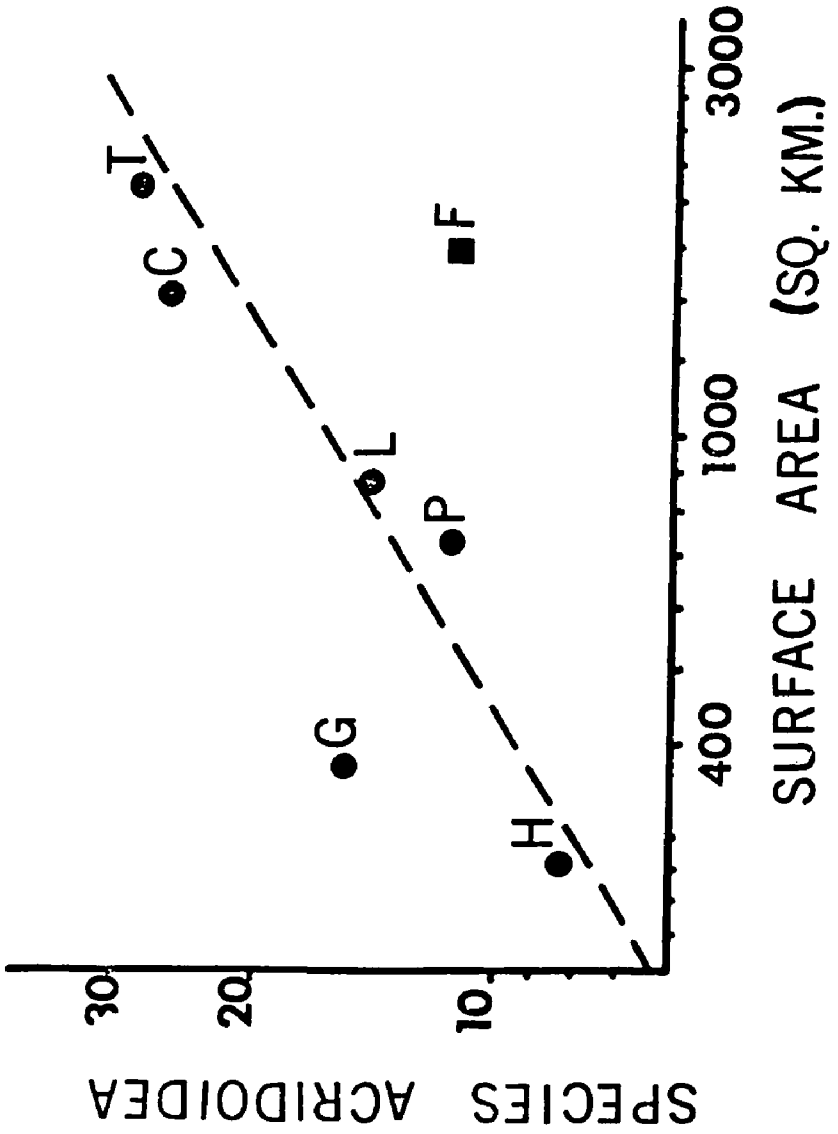
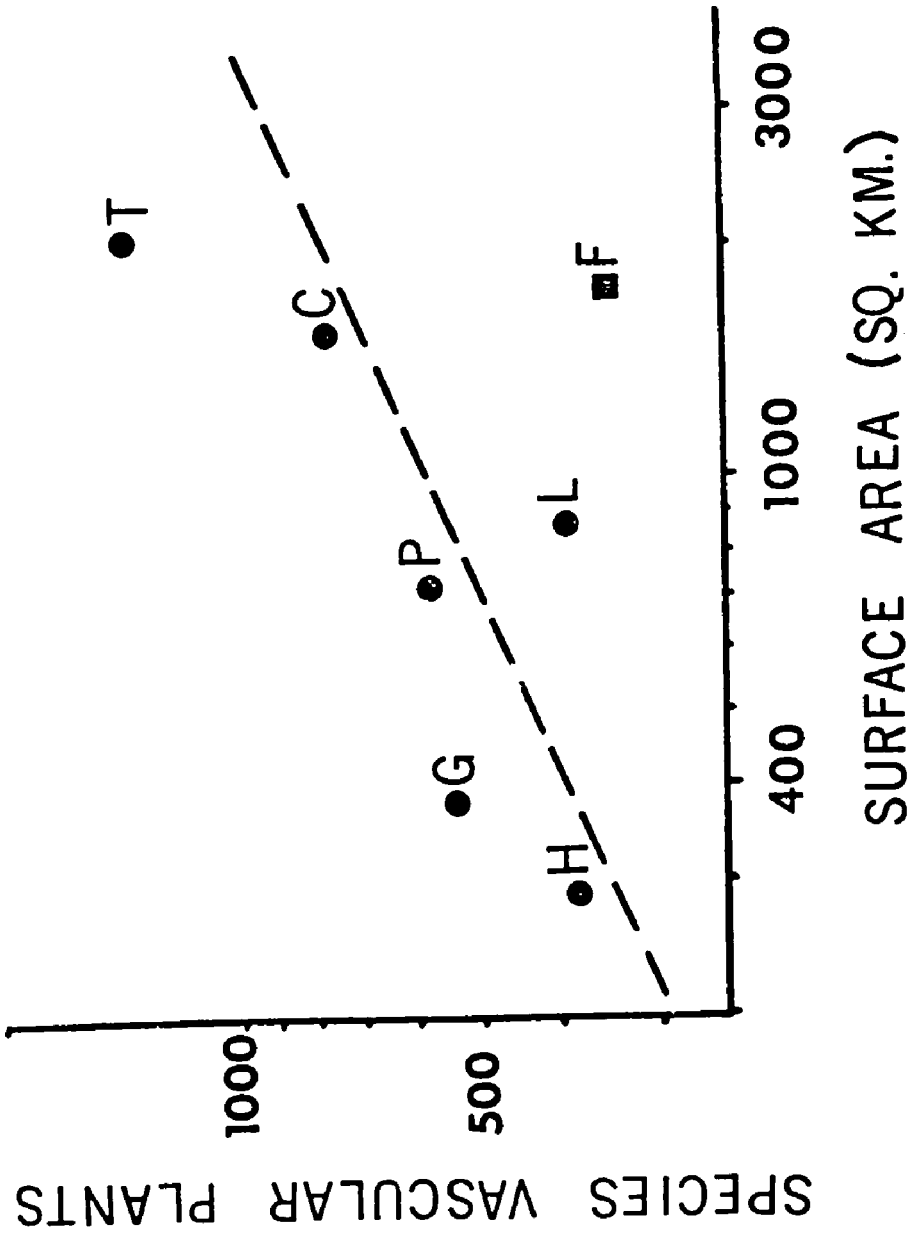

SPECIES ACRIDOIDEA
30
20
10
400
1000
3000
SURFACE AREA (SQ. KM.)
I
C
F
L
P
G
H

FIGURE 14. Species-area curve for the vascular flora of the Canary Islands. The coefficient of correlation is 0.590. $z = 0.424$ where $S = CA^Z$ and where S is the number of species on an island, A is the surface area of the island, C is a constant, and Z is a measure of floral increase with size (MacArthur and Wilson, 1967).


SPECIES VASCULAR PLANTS
1000
500
400
1000
3000
SURFACE AREA (SQ. KM.)
T
C
F
L
P
G
H

however, does not seem to be related to the diversity of the Acridoid fauna or the vascular flora on the Canary Islands (-.268 and -.163 respective coefficients of correlation).

Koopman (1958) studied the relative roles of geographic barriers and ecology in determining the faunal composition of the Caribbean Islands. On these islands, ecology (in particular vegetation type) was the primary determinant of bat diversity. Table 23 shows a very high correlation between species diversity of plants and Acridoidea on the Canary Islands, a result which may be interpreted causally. Although there is little doubt that the grasshopper fauna is dependent on the vegetation for food, the fact that the Oedipodine grasshoppers, which make up the largest portion of the Canarian grasshopper fauna, live in very open habitats, suggests that floristic diversity is not determining faunistic diversity in this system. Rather, I expect that this high correlation represents a similar response of both plants and grasshoppers to the same array of topographic features of elevation, dissection, distance from the mainland and area.

Island dissection would seem to be a critical factor in determining not only number of endemic species, but also total species diversity in as far as a topographically rigorous island may be expected to afford a more diverse assemblage of niches than a simple, flat island. Hence, an attempt was made to measure topographic dissection by quantitative means, and correlate dissection with species diversity. The most reliable means of estimating this parameter was found to be

determination of the total number of barrancos terminating at sea level per kilometer distance of perimeter. Precise and current geographic maps of the Canary Islands make this type of analysis possible.

The method is subject to error in that major volcanic eruptions tend to obliterate valleys. This objection seems to be a valid criticism of essentially any technique used to measure dissection since the complete geologic history of any island is unlikely to be determined. A similar technique of measuring complexity may be employed which is less precise than the perimeter method and subject to the same error, that of laying out a random grid system, covering the entire area of each island. This technique is less useful than the perimeter method since islands differ greatly in size. Only 10 complete 16 kilometer square grids may be laid out over the map of Gomera, but 46 grids of the same size will fit over the island of Fuerteventura. Whereas grid 2 will have a 10% chance of being sampled by random means for Gomera, grid 2 will stand only a 2% chance of being sampled for Fuerteventura. Further, peninsulas are rarely wide enough to fill a complete grid area, and therefore tend to be discounted.

Table 24 is a summary of average number of barrancos per kilometer perimeter for each of the seven major islands. Table 23 indicates that topographic dissection correlates very well with numbers of vascular plant species, and well with number of Acridoid species.

Elevation, another measure of ecological diversity, has a high correlation with topographic dissection (coefficient of correlation =

TABLE 24. Determination of island complexity in the Canaries.

Island	Number of barrancos terminating at sea level	Total distance around island (in km.)	Number of barrancos per km.
La Palma	162	119	1.4
Hierro	48	85	0.6
Lanzarote	26	150	0.2
Fuerteventura	153	242	0.7
Gran Canaria	189	167	1.1
Tenerife	431	236	1.9
Gomera	107	77	1.4

0.887; Figure 15). There is much expected redundancy in the ecology measured by these two estimates for several reasons, including the fact that a minimum elevation is required before cloud formation is possible which tends to produce barranco-forming run-off. The overlap in these two measures is clear when both are used in multiple regression analysis. The addition of either one as an independent variable when the other factor is already included, has essentially no effect on the multiple regression coefficient.

The factors of elevation and topographic dissection are more important in explaining the diversity of plants than of Acridoidea, although a positive linear slope is achieved in both (Figures 16, 17). This result is not unexpected; the distribution of many plant species is directly determined by specific features of the substrate. For example, a number of plant taxa are found only on the Tertiary rock outcrops in the Canary Islands, supposedly in response to specific mineral requirements (Lems, 1958).

Considering the overall system of topographic correlation with species diversity of vascular plants and grasshoppers on the Canary Islands, when studied singly, several conclusions may be drawn: 1) The flora and fauna studied seem to respond similarly to topographic features. 2) Nearest neighbor, area below the cloud belt and distance from the mainland have little effect in determining species diversity. 3) Elevation and topographic dissection are the best indicators of species diversity in the vascular plants of the Islands, although surface

FIGURE 15. Relationship between elevation and island complexity. The coefficient of correlation is 0.878. b = 0.167; m = 0.0005 where y = mx + b.

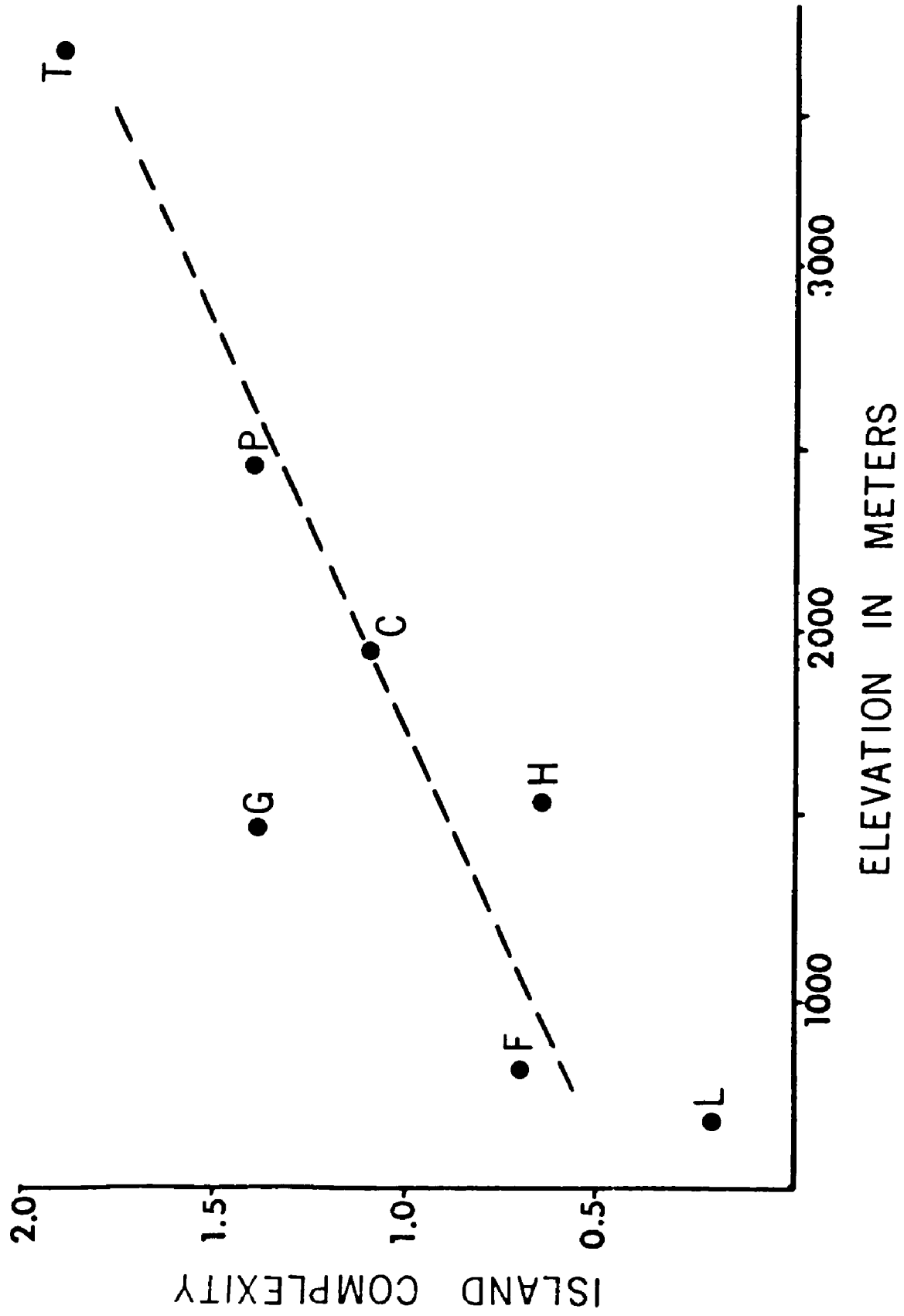

ISLAND COMPLEXITY
2.0
1.5
1.0
0.5
1000
2000
3000
ELEVATION IN METERS
T
P
C
G
H
F
L

FIGURE 16. Relationship in the Acridoidea between number of species and elevation. The coefficient of correlation is 0.624. b = 8.051 and m = 0.0042 where $y = mx + b$.

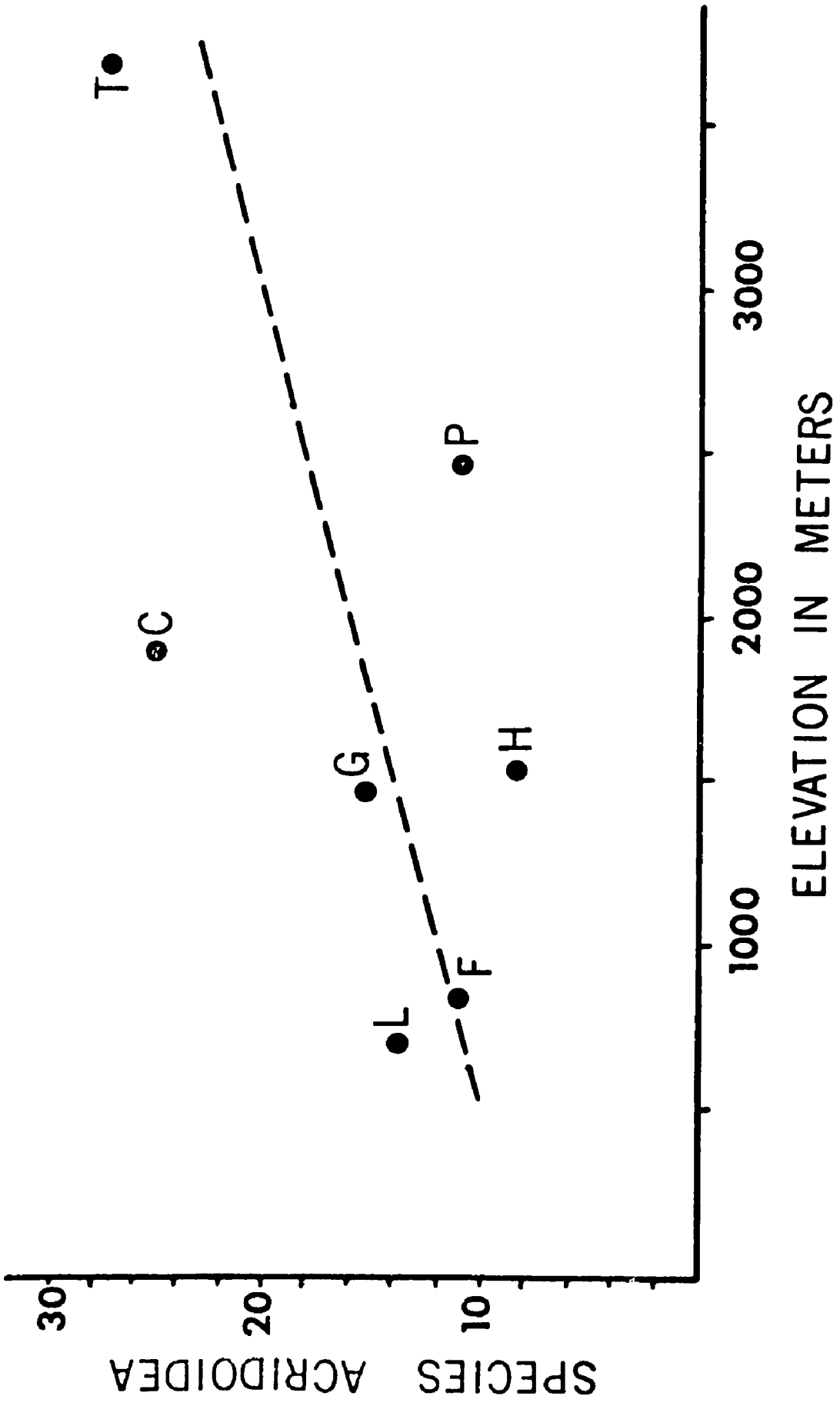
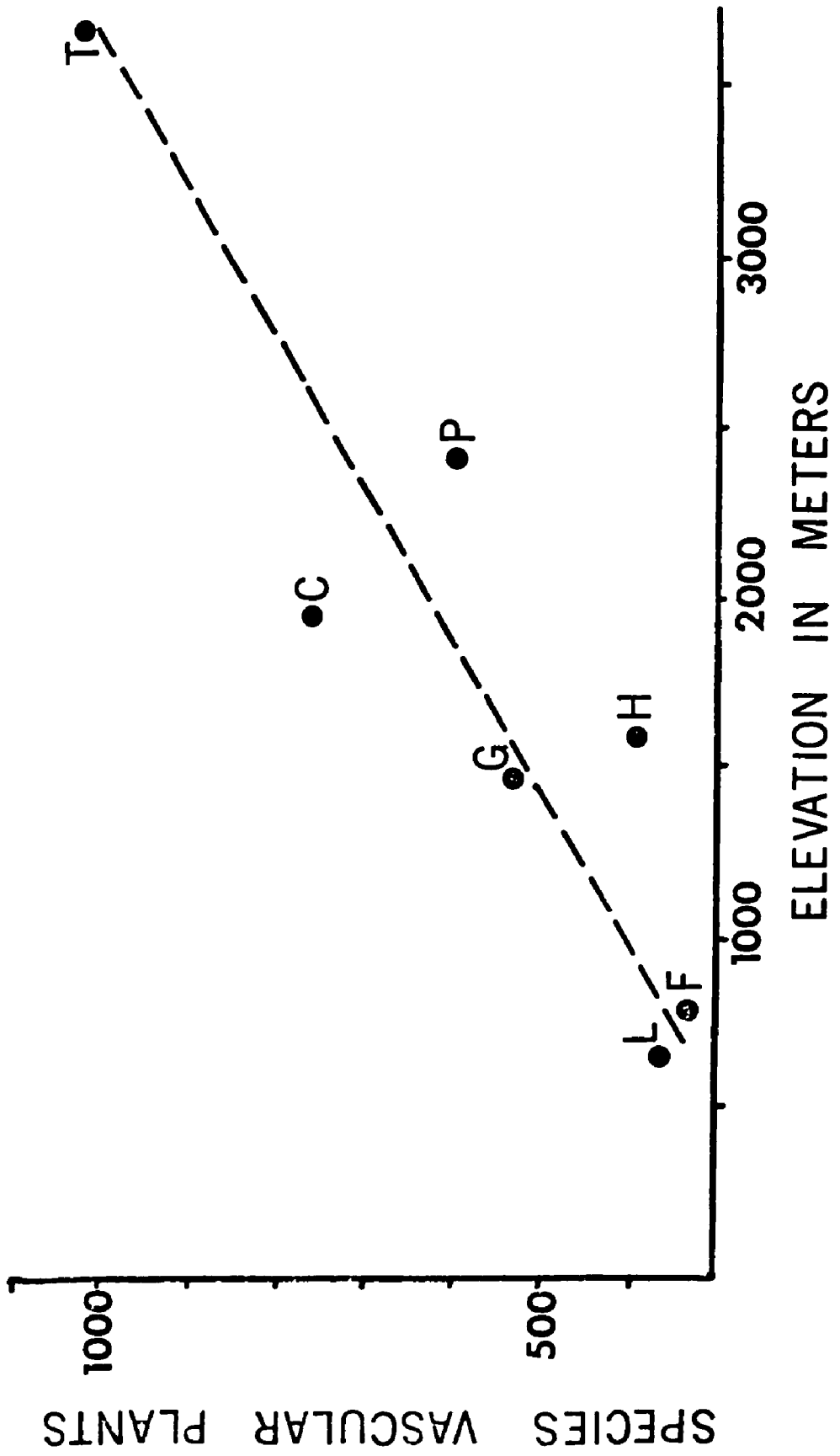

SPECIES ACRIDOIDEA
30
20
10
1000
2000
3000
ELEVATION IN METERS
T
C
P
G
H
L
F

FIGURE 17. Relationship in the vascular plants between species diversity and elevation. The correlation coefficient is 0.911. b = 165.37 and m = 0.2298 where $y = mx + b$.


SPECIES VASCULAR PLANTS
1000
500
ELEVATION IN METERS
1000
2000
3000
T
P
C
H
G
F
L

area is also important in this system. 4) Elevation, topographic dissection and surface area are about of equal importance in explaining Acridoid diversity.

Hamilton et al. (1964, 1965, 1967) have used methods of multiple regression analysis to consider the evolutionary problem of relative importance of various topographic features in determining species diversity. Hamilton, Rubinoff, Barth and Bush (1963) have shown that elevation is the major factor influencing numbers of plant species on the Galápagos, and Hamilton and his co-workers have shown that in the case of polyphyletic assemblages of bird species on archipelagos in the East Indies, East Central Pacific, West Indies and the Gulf of Guinea, area of island is the major indicator of species number (80-90%) when considered along with elevation of island (2-15%) and various measures of isolation (Hamilton and Rubinoff, 1963, 1964, 1967; Hamilton and Armstrong, 1965).

I have subjected the topographic factors for which I have data to multiple regression analysis. The factors of likely biological importance in this system for Acridoidea (Table 23) were elevation or topographic dissection, total surface area, distance from the mainland and area below the cloud belt. The relative importance of elevation, total surface area and distance from the mainland were studied for predictive ability in estimating numbers of plant species.

The resultant multiple correlation coefficients were high in both analyses (Acridoidea 0.993; vascular plants 0.967), indicating that

the combination of factors studied had high predictive value in estimating the dependent variables in question, number of species of Acridoidea and number of species of vascular plants, respectively.[11]

Within the limitations of multiple regression analysis, several conclusions can be made about the relative importance of topographic features in determining numbers of species of Acridoidea and vascular plants on the Canary Islands. It was found that species diversity of Acridoidea was affected approximately 48% by surface area available for habitation, 38% by elevation, about 12% by area under the clouds and less than 1% by distance from the mainland. Number of species of vascular plants may best be predicted by knowing the maximum elevation (82%), and to a lesser extent island area (35%). Again, distance from the mainland is rather unimportant in determining total numbers of species present (8%).

These results agree well with those of Hamilton and associates, for the flora of the Galápagos and the bird faunas of multiple tropical archipelagos, that elevation accounts for the greater part of variation in vascular plant diversity whereas area accounts for most of the variation in bird fauna diversity, with elevation of secondary importance.

The importance of elevation and surface area in determining

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[11] Only elevation and topographic dissection had significant F-values at $P = <.01$, while none of the correlations between topographic features and species diversity of Acridoidea were significant at this high level. This is probably a function of sample size ($N = 7$) which is not adjustable since there are only seven habitable islands in the Canarian archipelago.

species diversity may be tested in another independent analysis, that of calculating a ratio of factors and comparing this ratio with a third variable. For example, we know that the effect of distance per se is negligible in predicting total number of species on the Canary Islands. If area and elevation are indeed the factors that are producing this unexpected result, then removing the effects of area and elevation by constructing a ratio between species diversity and elevation or species diversity and area, and plotting these data against distance should show the predicted negative linear slope.

Figure 18 through 21 show that in all cases when species number is adjusted with area or elevation, the predicted decrease in number of species as distance from the mainland is increased is achieved.

FIGURE 18. Relationship in the Acridoidea between species diversity, elevation and distance. $r = -0.860$. $b = 0.0241$ and $m = -0.00005$ where $y = mx + b$.

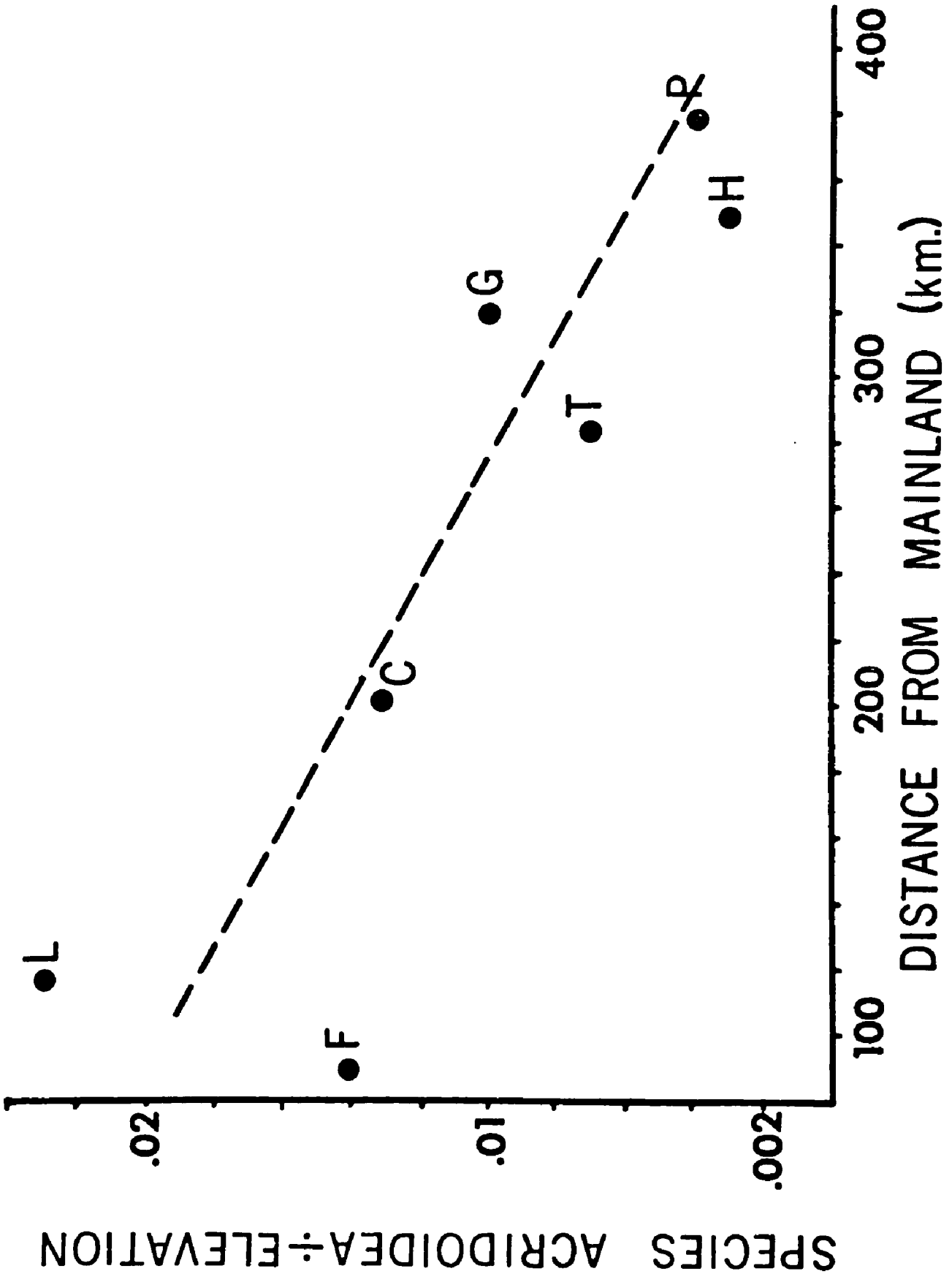

SPECIES ACRIDOIDEA÷ELEVATION
.02
.01
.002
100
200
300
400
DISTANCE FROM MAINLAND (km.)
L
F
C
G
T
H
R

FIGURE 19. Relationship in the vascular plants between species diversity, elevation and distance. $r = -0.8788$. $b = 0.5705$ and $m = -0.0008$ where $y = mx + b$.

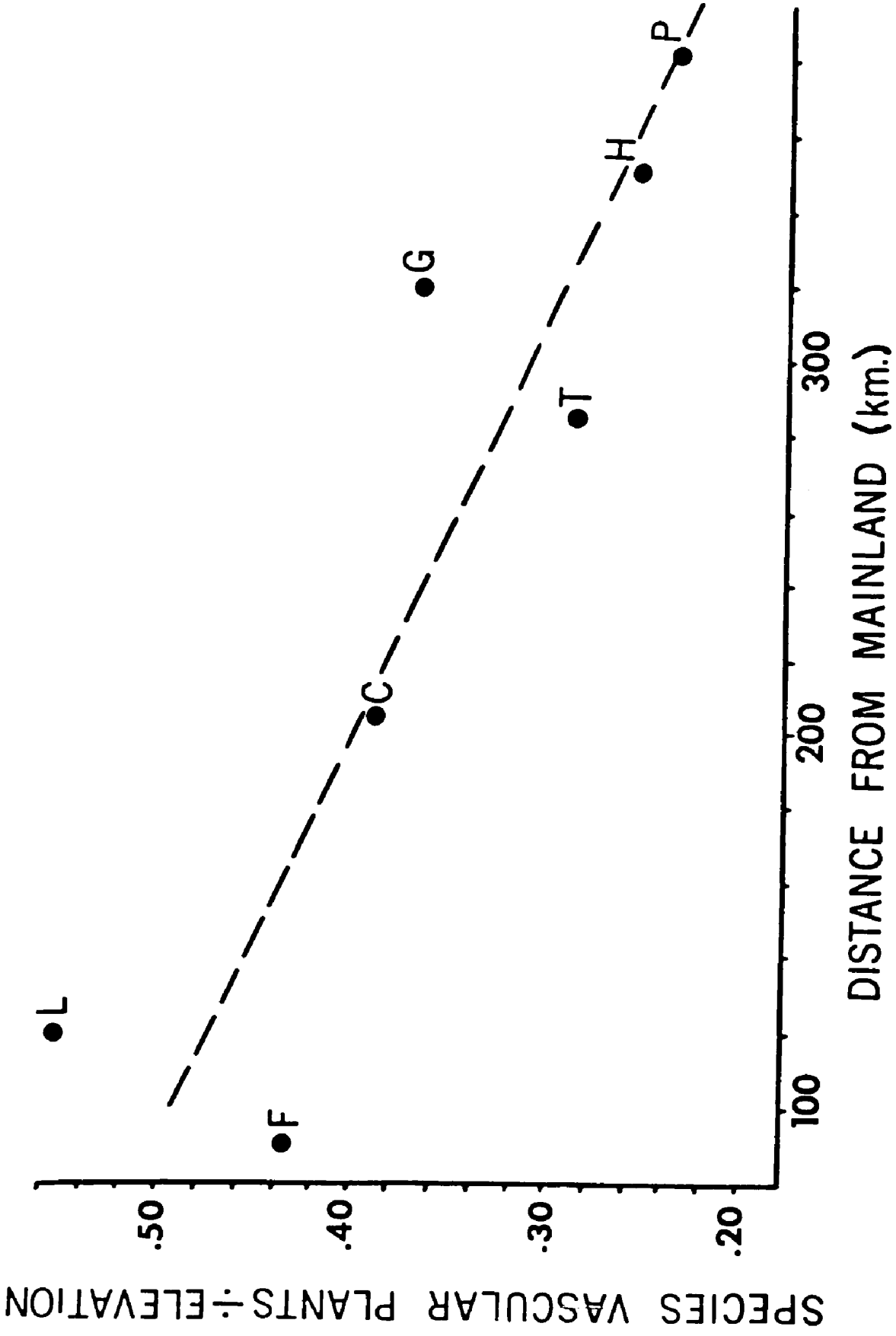

SPECIES VASCULAR PLANTS÷ELEVATION
.50
.40
.30
.20
100
200
300
DISTANCE FROM MAINLAND (km.)
L
F
C
G
T
H
P

FIGURE 20. Relationship in the Acridoidea between species diversity, area and distance. $r = -0.899$. $b = 0.025$ and $m = -.00005$ where $y = mx + b$.

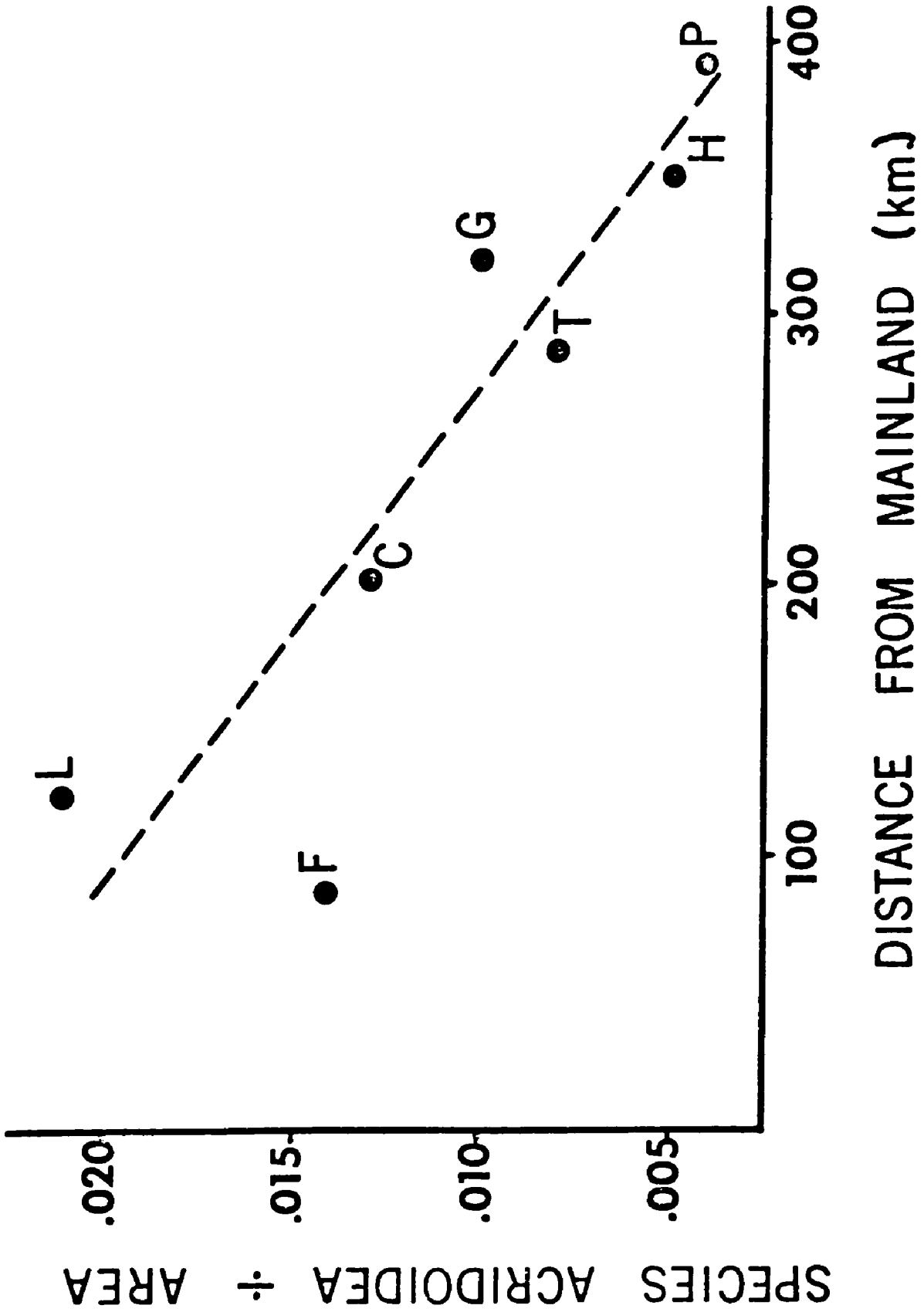
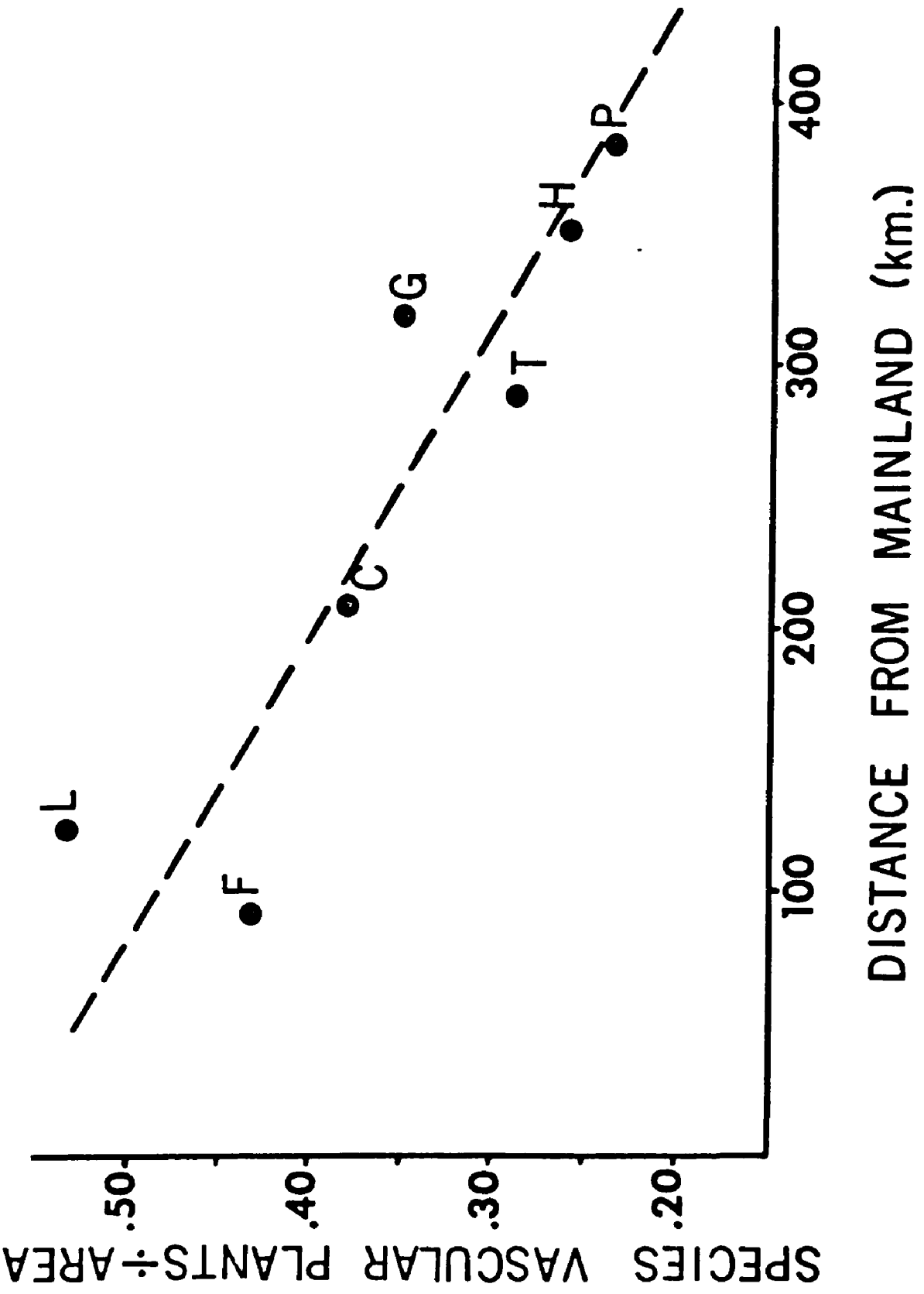

SPECIES ACRIDOIDEA ÷ AREA
.020
.015
.010
.005
100
200
300
400
DISTANCE FROM MAINLAND (km)
L
F
C
G
T
H
P

FIGURE 21. Relationship in the vascular plants between species diversity, area and distance. $r = -0.888$. $b = 0.556$ and $m = -0.0008$ where $y = mx + b$.


SPECIES VASCULAR PLANTS÷AREA
.50
.40
.30
.20
100
200
300
400
DISTANCE FROM MAINLAND (km.)
L
F
C
G
T
H
P

CONCLUSIONS

1. Forty-six species of Acridoidea (Orthoptera) are found on the Canary Islands. Twenty species (43%) are endemic to the Islands. Twenty-six species are nonendemic and occur on Africa or Eurasia or both.

2. It is likely that Africa is the major source area for the Acridoidea of the Canarian Archipelago. All of the nonendemic taxa known from the Canaries are found in Africa. Close relatives of endemic members also occur in Africa.

3. The Acridoid fauna of the Islands is taxonomically diverse. Although there are only 46 species, these represent a total of 10 subfamilies and 22 genera. Arminda, Sphingonotus and Wernerella are the only genera with more than three species each on the Islands, and all three have Canarian endemic members.

4. Grant (1966) implied that island size tends to influence the number of its congeneric species. However, on the Canary Islands, the proportion of congeneric species on each island is about the same, regardless of island size.

5. The insular distribution of endemic Acridoids is noteworthy. Lanzarote, the second closest island to the African mainland, has the lowest proportion of endemic species (14%). Gran Canaria, one of the three largest of the Islands, has the highest percentage of endemism (40%). All other islands, regardless of size and location have

approximately 25% endemics.

6. The distribution of endemic Acridoidea on and between islands is allopatric. In only two cases is more than one species of a genus established on any given island, and in these, the species have allopatric distributions on that island. The tendency towards allopatry is also seen in the Tettigoniine genus, Calliphona, which is endemic to the Canary and Madeira Islands.

7. The Acridoid fauna is most diverse between the xerophytic vegetation belt and 1500 meters. Only 4 of the 39 species classified according to occurrence in major vegetation zones are found above 1500 meters. Thirteen species may be found below the xerophytic belt on open beach.

8. If a species of Acridoidea is found in more than one vegetation zone, the zones are always adjacent; in no case is a species adapted to non-contiguous zones.

9. Twenty-two of the 46 known species occurring on the Canaries are known only from a single island. Of the species found on more than two islands, only one is endemic to the Canaries. All other taxa found on multiple islands are widely distributed on the mainland.

10. Several lines of evidence suggest that much of the Acridoid fauna of the Canary Islands is rather new. Although several endemic species have been taken rarely as erratics on adjacent islands, only five are established on more than a single island. These observations suggest that the

endemic fauna is in the expansion phase. As noted above, sympatry is the exception rather than the rule. Twenty-two of the 46 species are known from only a single island. Of these, nine are winged non-endemic forms, most of which I believe share gene pools with mainland counterparts. Among non-endemic species little morphological differentiation has occurred. Only in Dericorys has differentiation advanced to the subspecific level.

11. Although a number of wingless species occur on the Canary Islands, aptery in the Acridoids does not represent an adaptation to insular conditions. The closest relatives of the wingless species of the Canaries occur in continental Africa, and are themselves wingless or micropterous. In fact, there is a higher occurrence of reduced-wing taxa in the Acridoidea of Africa than on the Canary Islands.

12. Methods of multiple regression analysis were used to study the relationship between numbers of species of Acridoidea and vascular plants to topographic features of the islands. These features included surface area, distance from the mainland, maximum elevation, island complexity and nearest neighbor. It was found that, for the Acridoidea, number of species was affected about 48% by surface area available for habitation, 38% by elevation and less than 1% by distance from the mainland. Number of species of vascular plants may best be predicted by knowledge of the maximum elevation (about 80%), and to a lesser extent by surface area (35%). Again distance from the mainland is

rather unimportant in determining total numbers of species present. An independent method of testing the importance of area and elevation in this system was devised; results of these tests confirm the conclusions based on regression analysis.

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